

Figures 13, 14. Flowering and fruiting phenology. —Figure 13 (top). *Cydistia lilacina*. Based on 25 flowering and 12 fruiting specimens. —Figure 14 (bottom). *Cydistia potosina*. Based on 95 flowering and 11 fruiting specimens. Precipitation in cm is plotted 1.25× for Veracruz, Mexico, and 0.2× for Belize, Belize.

Table 1. Morphological/anatomical characters and character states for *Cydistia* and four genera that are presumably closely related (after Gentry, 1977a, 1997; Gentry & Tomb, 1979; Tomb & Gentry, unpublished).

	Tendrils	Phlo- em arms	Nectar disk	Corolla pubescence	Ovule organization	Fruit surface	Seed	Pollen aperture	Pollen exine
<i>Cydistia</i>	simple	8	absent	lepidote	2(-4)-seriate	smooth	bialate	inaperturate/ pericolpate	reticulate
<i>Roentgenia</i>	bi-trifid	8	absent	lepidote	2-seriate	smooth	bialate	3(-4)-colpate	reticulate
<i>Phryganocydia</i>	simple	8	absent	lepidote	2-seriate	smooth	corky	inaperturate	reticulate
<i>Clytostoma</i>	simple	8	absent	lepidote	2(-4)-seriate	echinate	corky	inaperturate	reticulate
<i>Potamogonos</i>	trifid	4	present	glabrous/ lepidote	4-seriate	?	?	3-colpate	reticulate

enas: Osa Peninsula near Rincón, 09°55'N, 84°13'W, *Gentry 1263* (MO). **San José:** Tabarcia, Bajo de los Bustamante, 09°51'N, 84°14'W, 840 m, *Solís 543* (CR-24222). PANAMA. **Bocas del Toro:** Río San Pedro, 08°49'N, 81°33'W, *Gordon 80C-a* (MO). **Canal Zone:** Barro Colorado Island, 09°11'N, 79°57'W, *Croat 11097* (SCZ). **Chiriquí:** Puerto Armuelles, 08°17'N, 82°52'W, *Croat 25036* (MO). **Coclé:** vicinity of El Valle, 08°37'N, 80°08'W, 600–1000 m, *Allen 1780* (F, GH, MO, NY, US). **Colón:** along roadside ca. 2 mi. E of Fort Sherman, 09°22'N, 79°57'W, *Gentry 733* (MO). **Darién:** El Real, 08°08'N, 77°43'W, *Gentry 4564* (MO). **Herrera:** 0.5 mi. E of Las Minas, 07°48'N, 80°45'W, *Gentry 3138* (MO). **Los Santos:** Punta Mala, 07°28'N, 80°00'W, *D'Arcy & Croat 4215* (MO). **Panamá:** Tocumen, 09°01'N, 79°23'W, *Dwyer 5130* (MO). **San Blas:** mountains above Puerto Obaldía, 08°40'N, 77°25'W, *Gentry 1477* (MO). **Veraguas:** Islas Contreras, Islo Brincaneo, 07°51'N, 81°47'W, 0 m, *Churchill 5711* (MO).

HAITI. Bayeux, Bord-de-la-mer, 19°49'N, 72°26'W, *Ekman H2669* (MO). DOMINICAN REPUBLIC. **Distrito Nacional:** Arroyo Tosa, 1.5 km from La Victoria on road to Mata Mamon, 18°36'N, 69°50'W, 10–20 m, *Mejía & Zanoni 9017* (MO). **El Seibo:** Laguna El Limón, 38 km E of Miches, 18°58'N, 68°51'W, 0–5 m, *Zanoni et al. 15883* (JBSD, MO). **Españat:** 8 km W de Gaspar Hernández, 19°38'N, 70°10'W, 10 m, *Gentry & Zanoni 50609* (MO). **María Trinidad Sánchez:** Llanura de Nagua, 29.4 km al NW de Nagua, 19°33'N, 69°55'W, 20–30 m, *Mejía & Pimentel 23630* (JBSD, MO). **Samaná:** en las orillas del Río Gran Estero, 13 km sureste de Nagua, 19°16'N, 69°46'W, *Zanoni et al. 30037* (MO). PUERTO RICO. Mun. of Fajardo, 1 km E of route 3, 18°17'N, 65°38'W, 30 m, *Miller & Sherman 6480* (MO); Guaynabo, Bo. San Patricio, 18°22'N, 66°06'W, *Otero 570* (MO). U.S. VIRGIN ISLANDS. **St. Croix:** 17°45'N, 06°45'W, *Benson 151-4124* (C). **St. Thomas:** Magens Bay, 18°17'N, 64°99'W, *Eggers 310* (FI, L). GUADELOUPE. 16°01'N, 61°31'W, *Isert s.n.* (C). DOMINICA. Coastal road between Batali River and Coulibistri, 15°30'N, 61°28'W, 0 m, *Ernst 1395* (MO). GRENADA. W. Ind. Woburn, 12°02'N, 61°44'W, *Broadway 1004* (L). MARTINIQUE. Environs de la case Pilote Mars, 14°35'N, 61°00'W, *Hahn 1407* (MICH). TRINIDAD AND TOBAGO. **Trinidad:** entrance to Caroni Swamp National Park, near Port of Spain, 10°32'N, 61°30'W, *Harriman 17563* (MO).

COLOMBIA. **Amazonas:** Leticia, 04°09'S, 69°57'W, 1974, *Gentry 12735* (COL, MO). **Antioquia:** Mun. de Sabanalarga, 8 km de Sabanalarga, 06°51'N, 75°49'W, 1100 m, *Callejas et al. 2238* (MO). **Atlántico:** Barranquilla Las Delicias, 10°58'N, 74°54'W, 1937, *Dugand 1135* (F, MO). **Bolívar:** near Cartagena, 10°28'N, 75°32'W, 10 m, *Gentry & Cuadros 47618* (MO). **Boyacá:** El Yopal, Llanos Orientales, 04°44'N, 72°15'W, *Blydenstein & Saravia 1251* (COL). **Caldas:** 14–21 km N of La Dorada on road to San Miguel, 05°27'N, 74°40'W, 330 m, *Gentry et al. 18150* (COL, MO). **Caquetá:** Cuernan, Río Caquetá, *Pabon 533* (ARAR). **Cesar:** 5 km W of Manaure, 10°22'N, 73°08'W, 440–460 m, *Gentry et al. 60737* (JBCGP, MO). **Chocó:** Ríosucio, Parque Natural Nacional Los Kaytos Cacarcas, 07°25'N, 77°10'W, 120 m, *León 338* (COL, MO). **Córdoba:** road from Fresquillo to Tierralta, 08°05'N, 76°10'W, 100 m, *Gentry & Cuadros 63956* (MO). **Cundinamarca:** 4 km W of La Mesa towards Tocaima, 04°38'N, 74°28'W, 900 m, *Gentry 15149* (COL, MO). **Guainía:** San Felipe, 01°47'N, 67°06'W, 120 m, *Gentry & Stein 46475* (MO). **Guavia-**

re: San José del Guaviare, 02°35'N, 72°38'W, 240 m, *Cuatrecasas 7473* (COL). **Magdalena:** Parq. Nac. Tairona, 50 m, *Gentry & Cuadros 47502* (JBCGP, MO). **Meta:** Mun. La Macarena, Río Guayabero 02°10'N, 74°06'W, 310 m, *Callejas & Marulanda 7118* (MO). **Nariño:** Tumaco, Mun. Espriella, 01°49'N, 78°46'W, *Romero-Castañeda 2793* (COL). **Norte de Santander:** Río del Oro, 09°09'N, 72°50'W, 40–50 m, *Garcta-Barriga & Lozano 18271* (COL, MO). **Santa Cruz:** 5 km WNW of Buena Vista, 17°27'S, 63°42'W, 350 m, *Nee et al. 36128* (MO). **Santander:** 51 km E of Barranca Bermeja toward Bucaramanga, 07°03'N, 73°52'W, 200 m, *Gentry & Forero 15351* (MO). **Sucre:** Coloso to Finca Sirena, along Quebrada El Salto, 09°30'N, 75°21'W, 300 m, *Gentry & Cuadros 68250* (MO). **Tolima:** Mariquita, 05°12'N, 74°54'W, 600–650 m, *Uribe-Uribe 3003* (COL). **Valle:** Armenia turnoff from Cali–Medellín hwy., S of Zarzal, 04°25'N, 76°05'W, 1000 m, *Gentry & Juncosa 40922* (MO). **Vaupés:** Río Kananari, Cachoera Palito, *Schultes & Cabrera 13126* (COL). **Vichada:** near Humaypia, Río Vichada, 04°55'N, 67°50'W, *Giovanni s.n.* (COL). EC-UADOR. **Napo:** 2–6 km above Puerto Bolívar, Río Cuyabeno, 00°06'S, 76°10'W, 300 m, *Brandbyge et al. 33731* (AAU, MO). **Pastaza:** Via Auca, 115 km al S de Coca, cerca del Río Tiguino, 01°15'S, 76°55'W, 320 m, *Rubio 121* (MO). **Sucumbíos:** Cuyabeno, 00°16'S, 75°53'W, 265 m, *Paz & Mino 81001* (MO). PERU. **Ju-nín:** Chanchamayo Province, Hacienda La Genoa, Finca Italia, 11°05'S, 75°25'W, 1150 m, *Gentry et al. 73439* (MO). **Loreto:** Requena, Sapuena, Jenaro Herrera, 04°50'S, 73°45'W, 170 m, *Vásquez et al. 10040* (MO). **Madre de Dios:** Tambopata, ca. 5 km from Puerto Maldonado, 12°35'S, 69°09'W, 200 m, *Gentry & Revilla 16281* (MO). **Pasco:** Cabeza de Mono, Río Iscozacín, 10°20'S, 75°18'W, 320 m, *Gentry et al. 41685* (MO). **Puno:** Río Távora, ridge top across from mouth of first major tributary, 13°21'S, 69°40'W, 500 m, *Gentry et al. 76897* (MO). **San Martín:** Tocache Nuevo, 08°10'S, 76°32'W, 450 m, *Gentry et al. 25480A* (MO). **Ucayali:** Coronel Portillo, Bosque Nacional de von Humboldt, 08°40'S 75°00'W, 270 m, *Gentry & Horna 29508* (MO). BOLIVIA. **Beni:** Yacuma, San Borja, 50 km hacia San Ignacio de Mojos, 14°49'S, 66°51'W, 250 m, *Beck 13215* (MO). **La Paz:** Alto Beni, 14°00'S, 65°30'W, *Seidel & Schulte 2324* (MO). **Pando:** Abuna Province, Nuevo Mundo, Campamento 18, 18 km N of airstrip, 10°39'S, 66°46'W, 160 m, *Gentry et al. 77759* (MO). **Santa Cruz:** Perseverancia, NW of Santa Cruz on Río Negro, 14°38'S, 62°37'W, 100 m, *Gentry & Mostacedo 73715* (MO). VENEZUELA. **Amazonas:** banks of the Río Manapiare, close to San Juan de Manapiare, 05°04'N, 66°03'W, *Berry 1593* (MO). **Anzoátegui:** km 227 on Caracas–Barcelona Hwy., 16 km E of Boca de Uchire, 10°08'N, 65°26'W, *Gentry & Berry 14833* (MO). **Apure:** Dto. San Fernando, 06°16'N, 67°31'W, 55 m, *Davidse & González 14363* (MO). **Aragua:** 8–9 km from the redoma at Cata Beach, SW towards Cuyaga, 10°29'N, 68°42'W, 400 m, *Holst et al. 2289* (MO). **Barinas:** 10–15 km W of Barinas, 08°38'N, 70°12'W, *Gentry & Puig-Ross 14263* (MO). **Bolívar:** Mun. Piar. Isla en el lago de Guri, 07°35'N, 62°58'W, 270 m, *Aymard et al. 10301* (MO). **Carabobo:** Bahía de Patanemo, 10°26'N, 67°55'W, *Delascio Chitty 2417* (MO). **Delta Amacuro:** Dept. Pedernales, Cano Angosturita, 09°52'N, 62°03'W, 50 m, *Steyermark et al. 114300* (MO). **Distrito Federal:** La Guaira, Est. Teleferico del Avila, 10°36'N, 66°56'W, *Plowman 7664* (MO). **Falcón:** Dto. Zamora, Cerro

Mampostal, 11°27'N, 69°17'W, 400 m, *González 1051* (MO'). **Guárico:** banks of Río Orituco, S of Calabozo, 08°45'N, 67°27'W, *Gentry 10263* (MO'). **Lara:** Jiménez Parq. Nac. Yacambu Qda. Honda, 09°41'N, 69°30'W, 700 m, *Davidse & González 21329* (MO'). **Mérida:** Santa María de Caparo, Dtto. Arzobispo Chacón, 08°30'N, 71°10'W, *López-Palacios & Bautista 3299* (MO'). **Miranda:** Cerros del Bachiller, 10 km of Cupira, 10°09'N, 65°48'W, *Steyermark & Davidse 116368* (MO'). **Monagas:** Río San Juan, Dtto. Benítez, Estado Sucre y Dtto. Maturin, Monagas, 09°24'N, 63°02'W, *Marcano-Berti 77-1-76* (MO'). **Portuguesa:** Dtto. Guanare. Colonia Agrícola, 09°07'N, 69°53'W, 200 m, *Aymard & Cuello 3566* (MO'). **Sucre:** Dtto. Benítez, E of Los Pozotes, 10°30'N, 63°07'W, *Steyermark et al. 121268* (MO'). **Táchira:** Dtto. Capacho, 07°52'N, 72°19'W, 1250 m, *Bono 4950* (MO'). **Trujillo:** Sabana Libre, 09°21'N, 70°39'W, *Christ 75* (VEN). **Zulia:** Dtto. Perijá, Carretera San Ignacio-Barranquitas, 10°00'N, 72°30'W, 125–150 m, *Bunting 5460* (MO'). GUYANA. **Demerara:** Demerara-Mahaica Region, along road from Cane Grove to Lamay Conservancy, 06°35'N, 57°50'W, 1–10 m, *Hahn et al. 3817* (MO'). **Essequibo:** W Demerara Region, W of Demerara River, 06°40'N, 58°11'W, 1 m, *Pipoly & Ameer 9110* (MO'). SURINAME. **Commewijne:** Zwamp, 140 m ten Noorden van Visserijzwamp, 05°01'N, 5°42'W, *Reijenga 57* (U). FRENCH GUIANA. **Cayenne:** Riviere de Kaw, 04°48'N, 52°09'W, *Granville 6848* (MO', U). **Inini:** Riviere Grand Inini, en amont de Saut Badjere, 04°39'N, 52°20'W, *Granville B-3728* (CAY, MO'). **Saül:** 03°38'N, 53°12'W, 220 m, *Gentry et al. 62974* (MO').

1B. *Cydista aequinoctialis* var. *hirtella* (Benth.)

A. H. Gentry, Ann. Missouri Bot. Gard. 60: 838. 1973. *Bignonia sarmentosa* Bertol. var. *hirtella* Benth., Bot. Voy. Sulphur 128. 1845. TYPE: Nicaragua. Realejo: *Hinds s.n.* (isotype?, K).

Bignonia sarmentosa Bertol., Fl. Guatimal. 25. 1840. *Cydista sarmentosa* (Bertol.) Miers, Proc. Roy. Hort. Soc. London 3: 191. 1863. TYPE: Guatemala. Esquintla: *Velásquez s.n.* (holotype?, BOLO).

Levyia nicaraguensis Bureau ex Baill., Hist. Pl. 10: 28–29. 1888. TYPE: Nicaragua. *Levy 38* (holotype?, P; isotypes?, F, K).

Arrabidaea guatemalensis K. Schum. & Loes., in Loes., Bot. Jahrb. Syst. 23: 129. 1896. TYPE: Guatemala. Bernoulli & Cario 2056 (holotype, K).

Arrabidaea pseudochica Kraenzl., Repert. Spec. Nov. Regni Veg. 17: 19. 1921. (fide Sandw., Kew Bulletin 22: 403–420. 1960.) TYPE: Mexico. Michoacán: *Langlassé 137, 506* (syntypes, K).

Anemopaegma tonduzianum Kraenzl., Repert. Spec. Nov. Regni Veg. 17: 116. 1921. TYPE: Costa Rica. Guanacaste: *Tónduz 13912* (isotypes?, K, P).

Cydista pubescens S. F. Blake, Contr. U. S. Natl. Herb. 24: 23. 1922. TYPE: Honduras. Copán: *Pittier 8488* (holotype?, US).

Description as in *C. aequinoctialis* except that the younger stems, petioles, petiolules, and veins of leaflets are conspicuously pilose.

Variety *hirtella* is restricted primarily to Mexico

and Central America (Fig. 3); only three collections are known from South America. The number of flowering specimens of *C. aequinoctialis* var. *hirtella* peaks in May (Fig. 9), whereas in variety *aequinoctialis* the peak is April (Fig. 8). Both varieties initiate flowering before the onset of the wet season in May, but flowering collections of variety *hirtella* drop sharply after May, and flowering collections of variety *aequinoctialis* remain common through August. These apparent differences in phenology may be a consequence of ecological diversification (Gentry, 1973a). However, few stable characters are available to distinguish the two varieties, and recognition at a higher taxonomic rank is not warranted at this time.

Representative specimens. MEXICO. **Chiapas:** Acala, *Laughlin 850* (DS, F, MEXU). **Guerrero:** Montes de Oca, Vallecitos, *Hinton 10219* (MO'). **Oaxaca:** 5 km N of Matias Romero, *King 808* (MICH). **Santiago:** Pinotepa, 16°19'N, 98°01'W, *Galeotti 7060E* (MO). **Veracruz:** Estación de Biología Tropical Los Tuxtles, 18°34'N, 95°09'W, 450 m, *Colín 144* (MO'). GUATEMALA. **Jutiapa:** Río Paz, *Heyde 6363pp* (MO). HONDURAS. **Comayagua:** Humuya River, *Hazlett 1099* (MO). EL SALVADOR. **Ahuachapán:** 0–2 mi. NE of San Francisco Menéndez, 200–450 m, *Croat 42068* (MO'). NICARAGUA. **Carazo:** between Amayito and Barranco, 11°40'N, 86°18'W, 30–300 m, *Stevens 22734* (MO'). **Chontales:** 0.6 km NE of Hwy. 7 on road to Comalpa, 12°10'N, 85°33'W, 160 m, *Stevens et al. 17177* (MO'). **Estelí:** Paso León, 3.9 km NNE of Hwy. 1 at Estelí, 13°08'N, 86°20'W, 815 m, *Stevens et al. 15487* (MO'). **León:** 4.0 SW of La Paz Centro, 12°18'N, 86°42'W, 35 m, *Stevens et al. 17243* (MO'). **Matagalpa:** carretera vieja a Jinotega, 800 m, *Moreno 22917* (MO'). **Nueva Segovia:** El Júcaro, 13°45'N, 86°06'W, 650–700 m, *Moreno 1693* (MO'). **Rivas:** Potrero Largo, 11°05'N, 85°42'W, 10–20 m, *Morales 2935* (MO'). **Rio San Juan:** San Miguelito, *Sandino & Martínez 3868* (MO'). COSTA RICA. **Guanacaste:** Isla San José, 10°53'N, 85°55'W, 50 m, *Janzen 12474* (MO'). PANAMA. **Darien:** Golfo de San Miguel, *Gentry 3957* (MO'). **Veraaguas:** ca. 11 mi. W of Sorá, *D'Arcy 5279* (MO').

COLOMBIA. **Chocó:** Bahía Solano, *Gentry & Fallen 17173* (MO'). **Santander:** Los Santos, Sabana de Torres, 328 m, *Renteria 202* (MEDEL). VENEZUELA. **Zulia:** 13 km N de Embalse, 10°25'N, 70°49'W, 550–600 m, *Bunting et al. 11268* (MO').

2. *Cydista decora* (S. Moore) A. H. Gentry, Selbyana 2: 42. 1977. *Anemopaegma decorum* S. Moore, Trans. Linn. Soc. London, Ser. 2. 4: 421. 1895. *Clytostoma decorum* (S. Moore) Bureau & K. Schum., in Mart., Fl. Bras. 8c: 151. 1896. *Arrabidaea decora* (S. Moore) Hassl., Spec. Nov. Regni Veg. Repert. 9: 49. 1910. *Clytostomanthus decorus* (S. Moore) Pichon, Bull. Soc. Bot. France 92: 224. 1945. TYPE: Brazil. Mato Grosso: *S. Moore 980* (holotype, BM; isotype, NY).

Lianas, stems tetragonal with four conspicuous

ridges, solid in cross section, drying gray to brown, glabrous; pseudostipules foliaceous, 2.5×2.0 cm, elliptic-orbicular, entire, glabrous. *Leaves* 8–13 cm long, bifoliolate with a simple, terminal tendril (or tendril scar); petioles 2–4 cm, sulcate, glabrate to puberulent, petiolules 1–4 cm, sulcate, glabrate to puberulent; leaflets 6–9 \times 3–7 cm, mostly narrowly to broadly ovate or ovate-elliptical, apices acute to acute-obtuse, bases obtuse or rounded, occasionally oblique, venation actinodromous basally and brochidodromous apically, 4–5 vein pairs, midrib and secondaries prominent, major veins puberulous beneath, isolated and scattered glands often in axils of secondary veins, margins slightly undulate, chartaceous. *Inflorescences* to 20 cm long, several-flowered, peduncles 3.0–7.5 cm, the rachis and peduncles conspicuously bracteate, the bracts 2–10 mm long, pedicels 5 mm long, sparsely lepidote, puberulent. *Flowers* ovoid in bud, apices straight; calyx 6–7 \times 5 mm, margins intact, apically truncate with five prominent mucronate teeth, 0.5–1.0 mm long, the whole with minute raised glands; corolla funnelform-campanulate, exserted 45 mm above level of calyx lip, 3–4 mm wide at calyx mouth, 15–20 mm wide at mouth, glabrate with short hairs in region of ovary; corolla lobes 20–22 \times 15–20 mm; stamens 15 or 22 mm long, shorter filaments inserted 1 mm and longer filaments inserted 5 mm above the level of the calyx lip, the staminode 5–6 mm long, inserted at the level of the calyx lip, anthers included; ovary 3 mm long, sparsely to densely lepidote, style 32 mm long, included. *Capsule* elongate-linear, 19–36 \times 1.2–2.0 cm, many-seeded; seeds flattened, 1–2 \times 3–4 cm, oblong with lateral membranous wings, each wing 1–1.5 cm long, margin subhyaline, 5–8 mm long, body ovoid, 2.0 \times 1.2 cm, not conspicuously bipartite, not well differentiated from wings. Figure: Gentry (1977a: fig. 10).

Cydista decora is one of only two *Cydista* species restricted primarily or exclusively to South America, where it inhabits two disjunct regions: (1) western Ecuador, and (2) portions of Bolivia, Paraguay, and southwestern Brazil (Fig. 4). The two *C. decora* populations differ in that the Ecuadorian collections possess conspicuously though somewhat inconsistently bracteate inflorescences (Gentry, 1977b). The peak in flowering collections occurs in March and appears to be correlated positively with rainfall (Fig. 10), but collections of fruiting specimens are too few to determine fruiting phenology.

The generic affinity of *Cydista decora* was uncertain before fruiting material was known. Once fruiting material was available, Gentry (1977b)

transferred it from the monotypic genus *Clytostomanthus* to *Cydista* and suggested that it may be closely related to *Cydista diversifolia*, although it differs, in part, by: (1) having larger flowers with a narrower calyx, (2) producing larger inflorescences, and (3) lacking glandular fields in the axils of the secondary veins beneath (although scattered, isolated glands are not uncommon). *Cydista decora* has more prominent calyx teeth than all other species in the genus.

Representative specimens. ECUADOR. **Chimborazo:** Río Chanchan, from Naranjapata to below Huigra, 02°16'S, 79°05'W, 2000–3000 m, *Camp E-3892* (F, US). **Esmeraldas:** W of San Mateo, Reserva Forestal de Jardín Tropical, 00°54'N, 79°37'W, 150 m, *Gentry & Lajones 73008* (MO). **Guayas:** Mocachi–Palenque, *Dodson et al. 14468* (MO). **Los Ríos:** Jauneche, 01°30'S, 79°25'W, 100 m, *Dodson et al. 7507* (MO). **Manabí:** vicinity of Agua Blanca, ca. 15 km of Puerto López, 01°28'S, 80°47'W, 590 m, *Hekker & Hekking 10259* (MO, QCA, U). BOLIVIA. **La Paz:** Alto Madidi, ridgetop ca 7 km NE of camp, 13°35'S, 68°46'W, 300 m, *Gentry & Estensoro 70713* (MO). **Santa Cruz:** San Juancito, 30 kms N de San Ignacio, 15°43'S, 67°16'W, 400 m, *Beck & Seidel 12407* (MO). PARAGUAY. **Amambay:** P. N. Cerra Corsa, Pedro Juan Caballero, 22°39'S, 56°03'W, 300 m, *Solomon et al. 7015* (MO, PY). **Canindiyu:** 34 km E of Villa Ygatimi near Río Jejui-mi, 24°08'S, 55°32'W, 150 m, *Gentry et al. 59301* (MO). **San Pedro Chore:** proximidades de la Colonia Aquidaban Nigui, 3 km N de la Ruta, 24°00'S, 57°00'W, *Davalos 3* (MO). BRAZIL. **Goiás:** Corumba, 15°55'S, 48°44'W, *Hoehne 5857* (R). **Mato Grosso do Sul:** Amambai, 3 km O Mato Grosso do Sul, 23°05'S, 55°13'W, *Hatschbach 45871* (MO). **Minas Gerais:** Corumba, *Hoehne 5858* (MO). **Paraná:** Porto São José, 22°43'S, 53°10'W, 246 m, *Hatschbach 5642* (MBM).

3. *Cydista diversifolia* (Kunth) Miers, Proc. Roy. Hort. Soc. London 3: 192. 1863. *Bignonia diversifolia* Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Quarto ed. 3: 133; Folio ed. 3: 104. 1819. *Pleonotoma diversifolium* (Kunth) Bureau & K. Schum., in Mart., Fl. Bras. 8: 274. 1897. TYPE: Mexico. Campeche: *Humboldt & Bonpland s.n.* (holotype, P).

Anemopaegma vargasianum DC., in A. DC., Prodr. 9: 190. 1845. *Cydista vargasiana* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 192. 1863. TYPE: Venezuela. Caracas: *Vargas s.n.* (holotype?, G-DC).

Bignonia sagreana DC., in A. DC., Prodr. 9: 148. 1845. TYPE: Cuba. *Sagra s.n.* (holotype?, G-DC; isotype?, K).

Lianas, stems tetragonal, hollow in cross section, drying light to dark brown with four distinct and light-colored ridges, puberulent; pseudostipules foliaceous, to 1.0 \times 1.5 cm, elliptic-orbicular, paired, entire. *Leaves* 8–12 cm long, once-pinnate with two primary, opposite leaflets and often a simple, terminal tendril; petioles 2–4 cm, sulcate, sparsely

lepidote, petiolules 1–3 cm, sulcate, sparsely lepidote; leaflets 5–8 × 4–7 cm, mostly ovate or ovate-elliptical, sometimes orbicular, apices acuminate to mucronate, bases truncate-rounded to slightly cordate, venation actinodromous (perfect, reticulate, basal) basally and brochidodromous apically, with 3–5 major veins, brown glandular fields often in axils of secondary veins, margins slightly undulate, chartaceous. *Inflorescences* to 20 cm long, several-flowered, peduncles 3.0–9.0 cm, the rachis and peduncles minutely bracteate, the bracts 1 mm long, pedicels 5 mm, sparsely lepidote-puberulent. *Flowers* ovoid in bud, apices straight; calyx 4–5 × 5–6 mm, generally drying uniformly dark, margin intact or shallowly split, apically truncate with five minute teeth; corolla funnelform-campanulate, exerted 35 mm past calyx lip, 4–5 mm wide at calyx mouth, 15 mm wide at mouth, glabrous except at fusion of filament and corolla tube where short, glandular hairs reside; corolla lobes 20–22 × 15 mm; stamens unequal, 13 or 16 mm long, inserted 1 mm below level of calyx lip, the staminode 6 mm long, inserted 1 mm below level of calyx lip, anthers included; ovary 3 mm long, lepidote, style 18 mm long. *Capsule* elongate-linear, 24–35 × 1.0–1.5 cm, reddish brown with inconspicuous longitudinal ridges, the central ridge most prominent, many seeded; seeds flattened, 1.0 × 3–4.5 cm, oblong with lateral membranous wings, each wing 1.2–1.8 cm long, body ovoid, 1.0 × 0.6 cm, clearly darker than wings, hyaline margin lacking.

Cydista diversifolia is a common liana, extending from the coastal regions of central Mexico to the Yucatán Peninsula and Cuba, and south through the Pacific side of Central America (Fig. 4). South American collections are restricted to central Colombia and northwestern and north-central Venezuela. Although it favors tropical dry forest, it may also occur in premontane moist and more infrequently tropical moist forests (Gentry, 1973b).

Gentry (1974) reported that *C. diversifolia* possesses a multiple-bang pollination syndrome and, like other species of *Cydista*, *C. diversifolia* apparently does not produce nectar and probably relies on deception of pollinators to effect pollen transfer. The number of flowering collections peaks in July or August (Fig. 11), and there are no significant phenological differences between Central and South American collections. Unlike other Mesoamerican *Cydista* species (*C. aequinoctialis*, *C. heterophylla*, and *C. potosina*), *C. diversifolia* initiates its peak flowering period after the onset of the wet season; flowering collections peak during the “ver-

nillo” or lull of the wet season. Fruiting collections peak between November and January (Fig. 11).

Cydista diversifolia differs from other species of *Cydista* in its hollow branchlets, a character not previously reported for this species (perhaps because this character is readily detectable only in cleanly cut branchlets). Venation in *C. diversifolia* is nearly palmate, with the five principal veins joining at the base of the blade.

Representative specimens. MEXICO. **Campeche:** 28 km N de Escarcega, rumbo a Champoton, 18°37'N, 90°43'W, *Cabrera et al.* 2045 (MO). **Chiapas:** Presa La Angostura, 45 km from Tuxtla, 16°34'N, 92°48'W, 700 m, *Breedlove* 37440 (DS, MO). **Guerrero:** El Pusulmiche, 3 km del Entronque de la Brecha a Corinto, Mun. Tecpan de Galeana, 17°15'N, 100°41'W, 60 m, *Tenorio et al.* 1348 (MO). **Jalisco:** La Huerta Est. de Invest., Exp. y Dif. Chabela, 19°32'N, 105°05'W, *Magallanes* 3150 (MO). **Michoacán:** 29 km al NE de Tumbiscatio, 18°31'N, 102°21'W, *Soto Núñez* 3644 (MO). **Oaxaca:** Cerro Arrenal, Tehuantepec, 16°20'N, 95°14'W, 1000 m, *MacDougall s.n.* (1971) (F, MO). **Quintana Roo:** 6 km N de Xel-Ha, 20°12'N, 87°20'W, *Téllez & Cabrera* 3229 (MEXU, MO). **Yucatán:** Chichén Itzá, 20°40'N, 88°34'W, *Gentry* 537 (MO). GUATEMALA. **Chiquimula:** between Chiquimula and La Laguna, 14°48'N, 89°33'W, 500–1000 m, *Steyermark* 30680 (F). **Izabal:** 25 km W of El Estor, 15°32'N, 89°21'W, *Harmon & Dwyer* 4319 (MO). **Petén:** along road on N shore of Lake Petén, 16°59'N, 89°50'W, *Croat* 24725 (MO). BELIZE. **Belize:** W of Benque Viejo near border with Guatemala, 17°06'N, 89°08'W, *Gentry* 8264 (F, MO). **Cayo:** Xuanantunich, Maya ruins just NW of Benque Viejo, 17°05'N, 89°08'W, *Ugent* 13 (MO, WIS). **Toledo:** 2–4 mi. W of San José Rd., 16°26'N, 89°02'W, 200–366 m, *Gentry* 8188 (MO). HONDURAS. **Choluteca:** vic. of Choluteca, 13°18'N, 87°12'W, 20 m, *Standley* 24406 (F). **Comayagua:** Los Manjas Station, 7 km N of Comayagua, 14°25'N, 87°37'W, 600 m, *D'Arcy* 18146 (MO). **Copán:** 4 mi. E of Copán, 14°50'N, 89°09'W, 800 m, *Croat* 42501 (MO). **Cortés:** Quebrada El Encanto, Montana la Cumbre, 15°30'N, 88°00'W, 200 m, *Molina* 3594 (F). **Morazán:** Río de la Orillo, 14°30'N, 87°00'W, *Rodríguez* 817 (F). **El Paraíso:** 15 km S of El Paraíso, 14°10'N, 86°30'W, 1300 m, *Molina* 18422 (F). **Valle:** Puerto de San Lorenzo, 13°30'N, 87°35'W, 0 m, *Molina* 5396 (F). **Yoro:** vic. of Coyoles, near Medina, 15°15'N, 87°15'W, 200 m, *Yuncker et al.* 8623 (F). EL SALVADOR. **La Libertad:** 6 mi. NW of La Libertad, 13°29'N, 89°19'W, *Wunderlin et al.* 743 (MO). NICARAGUA. **Boaco:** 4 km al S de Boaquito, San Antonio, 12°26'N, 85°44'W, 200 m, *Moreno* 18011 (MO). **Carazo:** between Amayito and Barranco Bayo, 11°40'N, 86°18'W, 30–100 m, *Stevens* 22764B (MO). **Chontales:** Hda. Corpus W of Juigalpa, 12°07'N, 85°28'W, 100 m, *Stevens* 21785 (MO). **Estelí:** Mechapa, 3 km al N de la Trinidad sobre la carretera Panamericana, 12°59'N, 86°14'W, 700 m, *Moreno* 22436 (MO). **Granada:** Casa Tejas, 11°46'N, 85°54'W, 40 m, *Moreno* 17091 (MO). **León:** El Velero, at mouth of Estero San José, ca. 10 km by road S of Hwy. 32, 12°08'N, 86°45'W, 3 m, *Stevens* 23050 (MO). **Managua:** Carretera Panamericana, 12°21'N, 86°03'W, 90–100 m, *Moreno* 1215 (MO). **Masaya:** Laguna de Apoyo, 11°56'N, 86°04'W, 100 m, *Moreno* 3932 (MO). **Matagalpa:** Las Playitas de Moyua NE de Lago Moyua, 12°37'N, 86°04'W,

475 m, *Sandino & Guzmán 844* (MO¹). **Rivas:** El Coyol Tola–Las Salinas, 11°23'N, 85°58'W, 35 m, *Stevens 9745* (MO¹). COSTA RICA. **Alajuela:** Llanos de Turrúcares, 09°54'N, 83°33'W, *Pittier 16436* (CR, US). **Guanacaste:** Paloverde, OTS Field Station, 8 km W of Bagaces, 10°32'N, 85°18'W, 100 m, *Gentry et al. 71450* (MO). **Limón:** La Bomba–Cahuita, 09°44'N, 82°50'W, 20 m, *Gómez & Hampshire 20130* (MO). **Puntarenas:** Isla del Caño, 17 km NW of Pta. Llorona, 08°37'N, 83°44'W, *Janzen 11641* (MO). **San José:** La Garita–Alajuela en propiedad del ICE, 09°59'N, 84°20'W, *Poneda & FcoCiccía 4172* (WIS). PANAMA. **Canal Zone:** Boy Scout Camp road near Madden Lake, 09°15'N, 79°35'W, *Gentry 2480* (MO). **Colón:** Quebrada Ancha, 3 km N of Clement Plant, 4 km ENE of Buena Vista, 100 m, *Nee 9122* (MO¹). **Panamá:** Madden Lake, 09°15'N, 79°35'W, *Gentry 5012* (MO).

CUBA. Cienfuegos Central Soledad, 22°09'N, 80°27'W, *Howard 4785* (B, C, CLEMS, L, TEX-LL, MEXU, MI). **La Habana:** Sierra de Anafe, 22°55'N, 82°40'W, 200 m, *Gentry & Hammel 71228* (MO). **Las Villas:** Loma de Bauao, 20°28'N, 76°22'W, *León & Luna 21956* (HAC). **Matanzas:** Playa on road from Buryvaea, 23°02'N, 81°34'W, *Britton et al. 556* (CM). **Oriente:** Sabanaso, 20°48'N, 76°42'W, *Ekman 7433* (AAU, B). **Pinar del Río:** Sierra de Anafe, *Ekman 13029* (B, MO).

COLOMBIA. **Antioquia:** Currulao Nueva Antioquia, 11 km E-NE de Turbo, 08°06'N, 76°43'W, 45 m, *Callejas et al. 5011* (COL, MO¹). **Atlántico:** Usiacuri, camino de Isabel López, 10°45'N, 74°59'W, 100 m, *Dugand & García-Barriga 2323* (COL). **Bolívar:** Mun. Cartagena, Isla de Tierrabomba, 10°20'N, 75°32'W, 5–30 m, *Cuadros 4338* (MO¹). **Cesar:** Gamara, Pto. Nacional, 10°22'N, 73°08'W, 70 m, *Uribe-Uribe 2409* (COL). **Cundinamarca:** 14 km S of Melgar, 04°12'N, 74°39'W, 400 m, *Gentry et al. 8972* (COL, MO). **Guajira:** Maicao, near El Ocho, 11°23'N, 72°13'W, *Bunch 212* (MO¹). **Huila:** 17.5 km N of Neiva, 03°02'N, 75°19'W, 640 m, *Croat 55260* (MO¹). **Magdalena:** Fundación, Santa Rosa, 09°25'N, 74°05'W, 200 m, *Romero-Castañeda 11055* (MO¹). **Norte de Santander:** Río Peralonso, alrededores de Santiago, 07°52'N, 72°43'W, 120 m, *Araque & Barkley 18NS104* (COL). **Santander:** 17 km NE of Socorro toward San Gil, 06°29'N, 73°16'W, 1250 m, *Gentry & Forero 15338* (MO¹). **Sucre:** Corozal, Palmitos, 09°19'N, 75°18'W, *Romero-Castañeda 9356* (COL). **Tolima:** Flandes, Finca San Rafael, 04°18'N, 74°49'W, 350 m, *Escobar et al. 158* (MED). **Valle:** Cali, 03°27'N, 76°31'W, 900 m, *Forero & Hernández 1555* (MO). VENEZUELA. **Aragua:** Tejería–La Encrucijada, 10°15'N, 67°10'W, *Aristeguieta 4311* (MO¹, VEN). **Carabobo:** Carretera de Maracay a Valencia, 10°05'N, 68°05'W, 400 m, *Williams 12193* (VEN). **Cojedes:** Via hacia Tinaco, cerca puente los Monos, 09°42'N, 68°26'W, 150 m, *Rojas 475* (MV). **Distrito Federal:** behind Univ. Católica Andrés Bello, Montalbán, Caracas, 10°30'N, 66°55'W, *Berry 1283* (MO¹). **Falcón:** Sierra de San Luis, carretera Coro–La Tabla, 11°07'N, 69°42'W, 600 m, *Flora Falcón 818* (MO¹). **Guárico:** 19 km N of Altigracia de Orituco, 08°21'N, 67°24'W, 500 m, *Gentry & Berry 15116* (MO¹). **Lara:** El Placer, cerca de Cabudare, 10°02'N, 69°16'W, 443 m, *Saer 621* (F, M, VEN). **Miranda:** Carretera Carenero–Chirimena, 2 km NW of Carenero, 10°32'N, 66°07'W, 0–5 m, *Steyermark & Bunting 102300* (NY, VEN). **Portuguesa:** 20 km al SO de Guanare, 09°03'N, 69°45'W, 200 m, *Aymard & Ortega 2844* (MO¹). **Táchira:** Matorrales, 07°52'N, 72°19'W, 1000 m, *Bono 5044* (MO¹). **Trujillo:** El Cenizo, 09°25'N, 70°30'W, 30

m, *Lasser 2832* (VEN). **Yaracuy:** Hacienda Iboa, near Guama, 10°20'N, 68°45'W, *Pittier 11158* (VEN US). **Zulia:** Dtto. Mara, Guasare–Socuy, 10°52'N, 72°29'W, 100 m, *Bunting 10319* (MO¹).

4. ***Cydista heterophylla*** Seibert, Publ. Carnegie Inst. Wash. 522: 417. 1940. TYPE: Mexico. Yucatán: *Lundell & Lundell 7350* (holotype, MICH; isotypes, A, F, US).

Bignonia lepidota Seem., Bot. Voy. Herald 179. 1854, non Kunth. TYPE: Panama. Isla de Iguana: *Cuming 1262* (isotype?, K).

Lianas, stems terete, solid in cross section, drying gray to brownish, inconspicuously lenticellate, glabrous; pseudostipules inconspicuous. *Leaves* 11–17 cm long, once-pinnate with two primary, opposite leaflets and often a simple, terminal tendril; petioles 2–3 cm, sulcate, sparsely puberulent, petiolules 2–3 cm, sulcate, sparsely puberulent; leaflets 7–12 × 4–7.5 cm, ovate to ovate-elliptic, apices acuminate to acute, bases obtuse or rounded, venation actinodromous basally (three principal veins conjoining) and brochidodromous apically, 3–4 vein pairs, glandular fields in axils of secondary veins inconspicuous and infrequent, margins slightly undulate, chartaceous. *Inflorescences* to 14 cm long, several- to many-flowered, peduncles 0.3–1.0 cm, the rachis and peduncles minutely bracteate, bracts 1 mm or less, pedicels 11 mm, lepidote. *Flowers* ovoid in bud, apices straight; calyx 4–5 × 4–5 mm, generally drying uniformly dark, margin shallowly split, sometimes appearing bilabiate, teeth lacking, densely lepidote; corolla funnelform-campanulate, exerted 40 mm above level of calyx lip, 2–3 mm wide at calyx mouth, 15 mm wide at mouth, glabrous; corolla lobes 15 × 15 mm; stamens unequal, 11 or 16 mm long, inserted 5 mm above level of calyx lip, the staminode 3 mm long, inserted 4 mm above level of calyx lip, anthers included; ovary 3 mm long, lepidote, style 28 mm long, included. *Capsule* elongate-linear, 20–35 × 1.7–2.0 cm, brown with minute dark glands and two conspicuous darkened submarginal ridges, many seeded; seeds 1.5 × 7 cm, oblong with lateral membranous wings, 3.0–3.5 cm long, becoming hyaline 5–8 mm from margin, body ovoid, not well differentiated from wings, not obviously bipartite but the dark midline extending 1/3 length of body. Figures: Gentry (1973b: fig. 10, p. 841), Gentry (1982: fig. 10, p. 101).

Cydista heterophylla is a common liana of tropical dry forests and drier areas of moist forests, occurring less commonly in moist regions (Gentry, 1973b). Its range extends from central Mexico to

the Yucatán Peninsula, south through Central America, and to the extreme northwestern portions of Colombia (Fig. 5).

Flowering is initiated prior to the onset of the wet season, and flowering collections peak in May, after which numbers of flowering collections decrease markedly (Fig. 12). Fruiting collections peak slightly from November to February (Fig. 12).

Seibert (1940) distinguished *Cydista heterophylla* by its conspicuously bilabiate calyces and production of flowers during the dry season while essentially leafless. Gentry (1973b) reported that *C. heterophylla* has "a propensity to simple leaves," and that the leaflets possess "a basal pair of arcuate veins with glandular fields in their axils." Many plants, especially juveniles, often exhibit two terminal pairs of simple leaves that mimic a whorl of four (Gentry, 1973b).

Representative specimens. MEXICO. **Campeche:** El Tormento, 5 km W of Escarcega, 18°37'N, 90°43'W, Held et al. FC86 (U). **Chiapas:** 5.6 mi. E of Chiapa de Corzo, 16°42'N, 93°00'W, 833 m, Breedlove 9559 (DS, F, MEXU). **Guerrero:** Zihuatenejo, rumbo a Isetla, 17°38'N, 101°33'W, German et al. 269 (MEXU). **Jalisco:** Puerto Vallarta, 20°37'N, 105°15'W, 16 m, Croat 45406 (MO). **Nayarit:** 6 mi. E of San Blas, 22°52'N, 105°06'W, Johnson 242-73 (MO). **Oaxaca:** Mun. Matías Romero, 8 km S de Esmeralda, 17°06'N, 94°48'W, 150 m, Wendt et al. 4809 (MO). **Quintana Roo:** En los alrededores de el Ramoral, 18°25'N, 88°30'W, Ramamoorthy et al. 2130 (MO). **Tabasco:** 10–40 km W of Huimanguillo, 17°51'N, 93°23'W, Barlow 30/161 (MEXU, MICH, WIS). **Vera-cruz:** Banos de Carrizal, 5 km SE of Emiliano Zapata, 19°20'N, 96°37'W, 220 m, Nee & Taylor 26601 (MO). **Yucatán:** near Xocenpich, 20°46'N, 88°35'W, Lundell & Lundell 7350 (A, F, TEX-LL, MICH, US). GUATEMALA. **Petén:** Santa Elena, Poctun, 16°06'N, 90°27'W, Tun 1189 (F, MO). BELIZE. **Cayo:** 4.5 km before Caracol, 16°46'N, 89°07'W, Balick et al. 3152 (MO). **Orange Walk:** Indian Church, 17°45'N, 88°40'W, Arnason & Lambert 17341 (MO). **Stann Creek:** Stann Creek Railway, 16°58'N, 88°13'W, 33 m, Schipp 224 (F, MICH, MO). **Toledo:** 2–4 mi. W of San José road, 16°15'N, 89°02'W, 200–366 m, Gentry 8192 (MO). HONDURAS. **Choluteca:** 5 km NW of San Francisco, 13°33'N, 87°16'W, Lent 598 (MO). **Comayagua:** La Cana, San Louis, 14°25'N, 87°37'W, 833 m, Edwards P-597 (F, MICH). **Copán:** Entre San Nicolás y Trinidad, carretera Santa Rosa de Copán, 14°57'N, 88°45'W, 100 m, Molina 11725 (F). **Cortés:** Entre Cofradía y Montana Cusuco, 15°30'N, 88°00'W, 1000 m, Molina 7302, (F). **Morazán:** Zamorano, 14°30'N, 87°00'W 850 m, Molina 115 (F). **Yoro:** Entre Yoro y Morazán, 15°15'N, 87°15'W, 700 m, Molina 6925 (F). EL SALVADOR. **La Unión:** Carretera a La Laguna de Olomega, 13°19'N, 88°04'W, Lagos 625 (MO). NICARAGUA. **Chinandega:** Camino de Puerto Morazán a Tonalá, 12°50'N, 87°09'W, 30–40 m, Sandino & Martínez 4363 (MO). **Chontales:** Camino entre Juigalpa y Puerto Díaz, 12°05'N, 85°24'W, 31–130 m, Guzmán et al. 373 (MO). **Estelí:** Mechapa, 3 km al N de La Trinidad sobre la carretera Panamericana, 12°59'N, 86°14'W, 700 m, Moreno 22435 (MO). **Granada:** Casa Tejas, 11°46'N, 85°54'W,

40 m, Moreno 17090 (MO). **León:** Quebrada of Las Ruedas, NW of El Tránsito, 12°05'N, 86°43'W, 15–30 m, Stevens et al. 20138 (MO). **Managua:** Carretera a Montelimar, 11°49'N, 86°31'W, 10 m, Guzmán et al. 438 (MO). **Masaya:** P. N. Volcán Masaya, 11°59'N, 86°10'W, 300 m, Neill 3135D (MO). **Matagalpa:** Puertas Viejas, 1–2 km camino a San José de los Remates, 12°35'N, 86°01'W, 430–470 m, Moreno 16263 (MO). **Nueva Segovia:** El Júcaro, Casa Viejas, 13°44'N, 86°05'W, 600 m, Moreno 13505 (MO). **Rivas:** Isla Ometepe, Volcán Maderas, Mérida, 11°27'N, 85°33'W, 240 m, Robleto 397B (MO). **Zelaya:** Kurinwacito, 13°08'N, 84°55'W, Moreno 23975 (MO). COSTA RICA. **Alajuela:** between Caldera and Orotina near Sitio Huacas, 09°54'N, 83°33'W, 150 m, Gentry et al. 71439 (MO). **Guanacaste:** Parq. Nac. Santa Rosa road to Estero Real, 10°50'N, 85°35'W, 150 m, Huft et al. 2103 (MO). **Puntarenas:** Barranca forest, vicinity of Miramar turnoff, 10°06'N, 84°44'W, Gentry 1332 (MO). PANAMA. **Canal Zone:** Barro Colorado Island, 09.11N, 79.57W, Croat 8206 (MO, SCZ). **Darién:** El Real, 08°08'N, 77°43'W, Gentry 4575 (MO). **Herrera:** 12.5 mi. E of Las Minas, 07°48'N, 80°44'W, Gentry 3143 (MO). **Panamá:** Río Espavé, 09°14'N, 78°46'W, Gentry 3700 (MO).

CUBA. **La Habana:** 23°08'N, 82°22'W, Sagra 89 (MO, F).

COLOMBIA. **Bolívar:** Mun. Turbaco, La Cantera de Cimaco, near Cartagena, 10°20'N, 75°25'W, 100 m, Gentry et al. 78483 (MO). **Sucre:** Estación de Primatos, 09°30'N, 75°30'W, 300 m, Gentry & Cuadros 68146 (MO).

5. *Cydista lilacina* A. H. Gentry, Mem. New York Bot. Gard. 29: 277. 1978. TYPE: Venezuela. Bolívar: Gentry, Morillo & de Morillo 10673 (holotype, MO; isotypes, MO, VEN).

Lianas, stems terete, solid in cross section, generally drying dark brownish green to dark gray, glabrous; pseudostipules inconspicuous. *Leaves* 20–25 cm long, once-pinnate with two primary, opposite leaflets and frequently a simple, terminal tendril; petioles 2.5–6 cm, inconspicuously sulcate, lepidote, petiolules 1.5–4 cm, conspicuously sulcate, lepidote; leaflets 11–19 × 5–14 cm, mostly broadly ovate-elliptical, occasionally ovate, apices obtuse-mucronate to acuminate, bases obtuse or rounded, occasionally oblique, venation actinodromous basally and brochidodromous apically, 4–5 vein pairs, midrib and secondaries prominent abaxially with dark confluent or isolated glands in axils of secondary veins, occasional dark glands throughout blade, margins slightly undulate, chartaceous. *In-florescences* to 19 cm long, several-flowered, peduncles 6.0–11.5 cm, the rachis and peduncles minutely bracteate, pedicels 5 mm, lepidote. *Flowers* ovoid in bud, apices curved; calyx 6–7 × 4.5 mm, drying uniformly dark, margin shallowly split, teeth five and minute, lepidote, ciliate with uniseriate hairs; corolla exerted 40 mm above level of calyx lip, 2–3 mm wide at calyx tip, 15 mm wide at mouth, stalked glandular hairs overall; corolla lobes

20–22 × 15 mm, irregularly elliptic; stamens unequal, 13 or 20 mm long, inserted 1 mm below level of calyx lip, the staminode 5 mm long, inserted 1 mm below level of calyx lip, anthers included; style 25 mm long, included; ovary 3 mm long, lepidote, ovules 4-seriate. *Capsule* elongate, 16–32 × 3–4 cm, surface wrinkled, many-seeded; seeds flattened, 1–2 × 4–5 cm, elliptic-oblong with lateral membranous wings, each 1.5–2.0 cm long, hyaline margin 3–5 mm, body ovoid, not clearly distinct from wings, bipartite with distinct longitudinal ridge. Figure: Gentry (1978: fig. 125).

Cydista lilacina is one of two almost exclusively South American *Cydista* species; a single collection from Costa Rica is known (Fig. 6). Collections are infrequent and distributed throughout South America north of Paraguay. *Cydista lilacina* is relatively common in only two regions: (1) northern Bolivia, eastern Peru, and western Brazil, and (2) eastern Venezuela. Flowering collections are few and appear to peak in October (Fig. 13). If this peak represents the true peak in flowering for the species, *C. lilacina* would be the latest-flowering species of the genus (precipitation was not plotted with phenology data because the paucity of and wide distribution of fertile collections precludes comparisons to any localized region).

Cydista lilacina differs from all other *Cydista* species in its 4-seriate ovules and curved bud apices. Capsules of *C. lilacina* and *C. potosina* are generally wider than those of all other species. However, the wrinkled surface of *Cydista lilacina* capsules differs from the smooth surface typical of capsules of *C. potosina* (Gentry, 1978). Vegetatively, *C. lilacina* resembles wide-leaved specimens of *C. aequinoctialis* but possesses round rather than sub-tetragonal branchlets.

Representative specimens. COSTA RICA. **Puntarenas:** Reserva Biologica Carara, 09°46'N, 84°29'W, 20 m, *Zúñiga 90* (CR, MO).

COLOMBIA. **Bolívar:** Santuario Nacional de Los Colorados, Mun. San Juan Nepomuceno, 09°58'N, 75°10'W, 230–250 m, *Gentry et al. 60654* (JBGP, MO). ECUADOR. **Pastaza:** 2 km del pueblo de Villano, 01°25'S, 77°20'W, 400 m, *Tipaz et al. 485* (MO). PERU. **Huánuco:** carretera Marginal, S of Bosque von Humboldt, 08°45'S, 75°01'W, 270 m, *Gentry & Jaramillo 41326* (MO). **Junín:** entre Santa Ana y Pampatigre, 11°50'S, 75°50'W, 900 m, *Fernández et al. 151* (MO, USM). **Loreto:** Dto. Calleria Bosque Nac. Alex. Humboldt, 250–300 m, *Schunke 10396* (AAU, MO). **San Martín:** 07°11'S, 76°33'W, 350 m, *Gentry & Smith 44983* (MO). **Ucayali:** Bosque von Humboldt, 08°40'S, 75°00'W, 250 m, *Gentry et al. 29527* (MO). BOLIVIA. **La Paz:** Alto Madidi across from mouth of Río Enlatagua, 13°35'S, 68°46'W, 280 m, *Gentry & Estensoro 70274* (MO). **Pando:** Carretera entre San Silvestre y Cu Curichon, 11°51'S, 68°37'W, *Beck et al.*

19589 (MO). SURINAME. **Nickerie:** Kabalebo Dam area, 03°34'N, 55°59'W, 30–130 m, *Lindeman & Roon 741* (MO). VENEZUELA. **Amazonas:** Dept. Atures, San Juan de Manapiare, 05°18'N, 66°03'W, 150 m, *Huber 1056* (MO). **Barinas:** Carretera La Yuca–Barinitas, 08°45'N, 70°25'W, *Marcano-Berti et al. 112-980* (IPA, MBM, MO, U). **Bolívar:** 2–15 km E of La Paragua–Ciudad Piar hwy., on road to San Pedro, 06°50'N, 63°20'W, 300 m, *Gentry & Berry 15063* (MO). **Delta Amacuro:** E of El Palmar, 08°20'N, 61°40'W, *Gentry & Berry 14987a* (MO). **Sucre:** Pen. Paria, between Guacoco and Guarataro, 10°43'N, 62°48'W, 80 m, *Steyermark & Liesner 121011* (MO). BRAZIL. **Acre:** on Río Branco Santa Rosa, 08°14'S, 73°13'W, *Lowrie et al. 440* (MO). **Amazonas:** basin of Río Jurua, near mouth of Río Embira, 07°30'S, 70°15'W, *Krukoff 5046* (MICH, MO, US). **Maranhao:** St. Luzia, Reserva Florestal de Buriticupu, 03°08'S, 42°54'W, *dos Santos et al. 70* (MO). **Mato Grosso:** Barra do Bugres, entre Denise e Arenapolis, 15°05'S, 57°11'W, *Saddi 4323* (CH). **Minas Gerais:** W side of Río Aripuana, below Salto dos Dardanelos, 20°41'S, 46°15'W, *Berg et al. P18531* (CH, MO). **Pará:** Parauapebas, Reserva Biologica da Serra dos Carajas, 07°45'S, 51°30'W, 600 m, *dos Santos et al. 218* (MO). **Rondônia:** Río Jaru, estrada Porto Velho–Cuiaba, 10°05'S, 61°59'W, *Duarte & Appa 7038* (MO, RB, INPA). **Roraima:** SEMA Ecological Station, Ilha de Maraca, 03°22'N, 61°25'W, *Ratter et al. R5373* (MO).

6. *Cydista potosina* (K. Schum. & Loes.) Loes., *Repert. Spec. Nov. Regni Veg.* 16: 209. 1919. *Arrabidaea potosina* K. Schum & Loes., *Bull. Herb. Boissier* 3: 618. 1895. TYPE: Mexico. San Luis Potosí: *Seler 616* (holotype, B not seen by Gentry).

Clytostoma mayanum Standl., *Carnegie Inst. Wash. Publ.* 461: 86–87. 1935. TYPE: Guatemala. Petén: Yaxha–Remate Road, *Lundell 4008* (holotype, F; isotype, S).

Lianas, stems tetragonal, solid in cross section, drying gray with four distinct and often light-colored ridges, glabrous; pseudostipules linear-triangular, numerous, overlapping, usually less than 8 mm long. *Leaves* 6–14 cm long, once-pinnate with two primary, opposite leaflets and often a simple, terminal tendril; petioles 1–4 cm, inconspicuously sulcate, puberulent, petiolules 1–4 cm, sulcate, puberulent; leaflets 4–10 × 2–5 cm, mostly ovate to ovate-elliptical, apices acuminate, bases rounded to obtuse, venation brochidodromous, 4–5 vein pairs, veins puberulent-pilose beneath, solitary glands in axils of secondary veins occasionally present, margins slightly undulate, chartaceous. *Inflorescences* to 10 cm long, ca. 4–8-flowered, peduncles 0.5–8.5 cm, the rachis and peduncles minutely bracteate, pedicels ca. 5 mm, lepidote. *Flowers* ovoid in bud, apices straight; calyx 2–7 × 5–6 mm, apically truncate with five minute teeth, drying dark basally and lighter apically, lepidote with dense aggregations of hair; corolla funnellform-campanulate, exerted ca.

35 mm above level of calyx lip, 2–3 mm wide at calyx mouth, ca. 15 mm wide at mouth, lepidote; corolla lobes 16 × 20 mm, irregularly elliptical; stamens 5, unequal, 10 or 17 mm long, filaments paired, distinct, adnate to corolla tube, shorter filaments inserted 2 mm and longer ones 5 mm above level of calyx lip, the staminode 3 mm long, inserted at level of calyx lip, anthers with two spreading thecae, subterminal on the filament; disk wanting, ovary 3 mm long, cylindrical, lepidote, style ca. 30 mm long, included, stigma bipartite, divisions laterally flattened. *Capsule* elongate, 20–24 × 2.8–3.2 cm, drying dark, surface smooth, many-seeded; seeds flattened, 1.5 × 6 cm, oblong with lateral membranous wings, each 1–2 cm wide, frequently unequal, margin hyaline, 1 mm or less, body ovoid, not obviously bipartite but with dark medial ridge extending ½ length of seed.

Cydista potosina (Fig. 1) has the most restricted distribution of all *Cydista* species (Fig. 6); it ranges from the southeastern half of central Mexico to the Yucatán Peninsula and Belize, with sporadic collections from Guatemala, Honduras, El Salvador, and Nicaragua. A single collection is known from Costa Rica. Gentry (1982) reported a “multiple-bang” flowering phenology in *C. potosina*. Flowering collections peak in June and decline sharply by August (Fig. 14). Like *C. aequinoctialis* and *C. heterophylla*, *C. potosina* appears to initiate flowering before the onset of the wet season. Fruiting collections are evenly distributed from September to March (Fig. 14).

Cydista potosina differs from all other *Cydista* species in its distinctive, bicolorous (when dried), ciliate-margined calyx. *Cydista potosina* and *C. lilacina* have capsules that are wider than those of other *Cydista* species. The branchlets of *C. potosina* and *C. decora* are tetragonal and frequently dark with four light-colored, longitudinal ridges. The leaflet venation of *C. potosina* more closely resembles the uniformly brochidodromous type of *Clytostoma*, rather than the basally actinodromous type of many *Cydista* species. The pseudostipules of *C. potosina* are reminiscent of the bromeliad-type clusters typical of *Clytostoma*, which further suggests a relationship between the two genera. However, the smooth, lepidote ovary and smooth fruit of *C. potosina* indicate a closer affinity to *Cydista* than to *Clytostoma*.

Representative specimens. MEXICO. **Campeche:** Hopelchen, 10 km de Xpujil, 18°12'N, 89°26'W, *Chan* 1289 (XAL-M). **Chiapas:** Chicomuselo, 15°46'N, 92°16'W, 650 m, *Matuda* 5652 (MEXU, TEX-LL). **Oaxaca:** Mun. M. Romero, 7.2 km O de Esmeralda, 17°08'N, 94°50'W, 100 m, *Wendt et al.* 3618 (MO¹). **Puebla:** M. Sn. Diego,

18°50'N, 98°00'W, *Ramírez* 258 (MEXU). **Quintana Roo:** 1 km NW of Puerto Morelos, 20°50'N, 86°52'W, 5 m, *Davidse et al.* 20022 (MO¹). **San Luis Potosí:** San Antonio, La Ladrillera, 22°08'N, 100°59'W, 300 m, *Alcorn* 3199 (MO¹). **Tabasco:** Cerro las Campanas, 3 km E of Teapa, 50 km S of Villahermosa, 17°33'N, 92°57'W, 50–100 m, *Conrad & Conrad* 2813 (MO¹, MEXU). **Veracruz:** Cerro El Vigía Estación de Biología Tropical Los Tuxtlas, 450 m, *Sinaca-Colin* 144 (MO). **Yucatán:** Chamul, village 8 km from Xuilub, 25m, *Mogensen* 1038 (MO¹). GUATEMALA. **Escuintla:** slopes of the Río Coyolate, 13°57'N, 91°19'W, *Harmon* 2379 (MO¹). **Izabal:** across bay from Puerto Barrios, 15°43'N, 88°36'W, 20–50 m, *Steyermark* 39853 (F). **Petén:** Remate, 13 km NE of Village, 17°00'N, 89°42'W, *Contreras* 927 (MO¹, TEX-LL). BELIZE. **Belize:** W of Spanish Lookout, road to ferry, 17°13'N, 88°59'W, *Dwyer et al.* 461 (MO). **Cayo:** near Teakettle, 17°14'N, 88°51'W, *Whitefoord* 3317 (MO¹). **Co-rozal:** 18°24'N, 88°24'W, *Gentle* 181 (MICH). **Stann Creek:** Cockscomb Mts, 16°48'N, 88°37'W, 100–166 m, *Gentry* 8001 (MO¹). **Toledo:** Southern Hwy., 14 mi. N of Punta Gorda–San Antonio, 16°15'N, 89°02'W, 100–166 m, *Gentry* 8228 (F, MO¹). HONDURAS. **Atlántida:** E of Tela near Yoro Trail, 15°44'N, 87°27'W, *Yuncker* 4973 (F, MICH, MO¹). **Yoro:** near the village of Los Flores, 15°15'N, 87°15'W, 950 ft., *Yuncker et al.* 8163 (MO¹). NICARAGUA. **Chontales:** 2.6 km NW of Cuapa, 12°16'N, 85°23'W, 500 m, *Stevens & Montiel* 17441 (MO). **Jinotega:** 21 km del Valle del Cua, NW de El Cedro, 13°30'N, 85°38'W, 700 m, *Moreno* 944 (MO¹). **Nueva Segovia:** Río Diplito, E de Ciudad Ocotol, 13°37'N, 86°27'W, *Sandino* 2995 (MO¹). COSTA RICA. **Puntarenas:** Parque Nacional Corcovado, Pavo Forest, 08°27'N, 83°33'W, 0–150 m, *Kernan* 573 (CR). EL SALVADOR. **Ahuachapán:** El Imposible, cerca de los Enganches, 13°52'N, 89°59'W, *Sermeno* 175 (MO¹). **La Libertad:** Hacienda La Argentina, 13°40'N, 89°20'W, 500 m, *Montalvo* 4267 (ITIC).

DUBIOUS OR REJECTED NAMES

Bignonia variabilis Seibert ex E. Mey., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 779. 1825. Pro syn., non Jacq. (1797).

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Collections are listed alphabetically by the principal author, followed by collection number, and a boldface number (1-6) designating the species collected. All specimens entered into TROPICOS were assumed to have been examined by A. H. Gentry. Specimens examined by the author were limited to duplicates housed at MO, and are indicated by a "!" in superscript. Collections cited under "representative specimens" are not included in the Index to Exsiccatae. The coding of the species numbers is as follows: **1a** = *Cydista aequinoctialis* var. *aequinoctialis*, **1b** = *Cydista aequinoctialis* var. *hirtella*, **2** = *Cydista decora*, **3** = *Cydista diversifolia*, **4** = *Cydista heterophylla*, **5** = *Cydista lilacina*, and **6** = *Cydista potosina*.
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Ibarra-Manríquez & Sinaca 1752' 6; Idrobo 1516 3, 1508 3; Idrobo et al. 1319 1a; Ijjasz-Madriz 478 1a; Iltis 27284a 3; Iltis & Nee 1469 1a; Irwin et al. 48056 1a, 47425 1a, 47575 1a, 48055 1a, 48056 1a, 48789 1a, 48790 1a, 53349' 1a, 55529' 1a, 55544' 1a; Isert s.n. 1a.

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SYSTEMATICS OF *ELEUSINE*
GAERTN. (POACEAE:
CHLORIDOIDEAE):
CHLOROPLAST DNA AND
TOTAL EVIDENCE¹

Khidir W. Hilu² and John L. Johnson³

ABSTRACT

Eleusine (Poaceae) comprises four annual and five perennial species, which are primarily East African except for the vicariant *E. tristachya*, a widely distributed species in South and Central America. Taxonomic difficulties in the genus have been attributed to active speciation in the early stages. *Eleusine* includes an allotetraploid African and Indian cereal, *E. coracana* subsp. *coracana*, a taxon with an incompletely resolved origin. Chloroplast DNA restriction site variation is used here to elucidate the phylogenetic relationships among species of *Eleusine*, assess the affinity of *E. multiflora* to the genus, and provide additional input into the origin of polyploid *E. coracana*. Chloroplast DNA data confirm the monophyly of the annuals *E. coracana*, *E. indica*, and *E. tristachya* and support the inclusion of the annual *E. multiflora* in the genus as a separate entity. The perennial species appeared paraphyletic. Information from the chloroplast genome is in general agreement with previous molecular, biochemical, and cytogenetical studies on the genus. The present investigation provides additional support for the origin of the crop from the tetraploid *E. coracana* subsp. *africana* and substantiates the monophyly of the two subspecies of *E. coracana* and *E. indica*. Evidence presented points to the African origin of the vicariant *E. tristachya* and an earlier introduction to and further differentiation in South America.

Eleusine Gaertn., Poaceae subfamily Chloridoideae, is comprised of four annual and five perennial species (Phillips, 1972). Polyploidy (both euploidy and aneuploidy) has played a role in the evolution of the genus with the evident presence of diploids and polyploids based on basic chromosome numbers of $x = 10, 9,$ and 8 (Hiremath & Chennaveeraiah, 1982; Hiremath & Salimath, 1991). Clayton and Renvoize (1986) indicated that active speciation has made the genus taxonomically difficult. *Eleusine* has a center of diversity in East Africa where eight of its nine species occur. The exception is *E. tristachya* (Lam.) Lam., which occurs from South America north to the southwestern United States, and as a rare adventive in East Africa (Hilu, 1980).

Phillips (1972) arbitrarily divided *Eleusine* into two groups, annuals and perennials. Among annuals, the taxonomic affinity of *E. multiflora* Hochst. ex A. Rich. to the other species was questioned originally on the basis of morphological information (Phillips, 1972; Hilu & deWet, 1976a). However,

isozyme information (Werth et al., 1994) points to close affinity between *E. multiflora* and other species of *Eleusine*. The remaining annual taxa include *E. coracana* (L.) Gaertn. subsp. *coracana*, an important East African and Indian crop known as finger millet. The crop is believed to have been domesticated from *E. coracana* subsp. *africana* (Kennedy-O'Byrne) Hilu & deWet (Chennaveeraiah & Hiremath, 1974; Hilu, 1988). Isozyme information, on the other hand, raised the point that subspecies *africana* may not be the direct ancestor of the crop (Werth et al., 1994). This hypothesis and the unknown identity of one of the diploid parents leave unresolved questions about the origin of tetraploid *E. coracana*.

Among the perennials, *E. semisterilis* S. M. Phillips has been described from a single specimen collected from the southeastern part of Kenya, near Mombasa (Phillips, 1972), and possibly has become extinct. The remaining perennial species have wider geographic distributions in East Africa.

¹ We thank D. M. Porter for comments on a draft of the manuscript, T. H. N. Ellis (John Innes Institute) and A. Day (University of Geneva) for providing the chloroplast DNA clones, the U.S. Department of Agriculture Southeastern Regional Plant Introduction Station for providing some of the seed collections used in the study, and two anonymous reviewers for their comments. This research was supported under grant No. DHR-5600-G-00-1073-00, Program in Science and Technology Cooperation, Office of the Science Advisor, U.S. Agency for International Development, and The International Board of Plant Genetic Resources grant 85/49.

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Table 1. Species, chromosome numbers, plant collections used in the study, and sources of the material. The PI numbers refer to the U.S. Department of Agriculture collections (USDA), and the KH numbers designate K. Hilu collections. Voucher specimens are located at VPI.

Species	Collection number	Geographic origin	Chromosome number (2n)
<i>Eleusine coracana</i> subsp. <i>coracana</i>	USDA, PI231130	Fort Portal, Uganda	36
<i>E. coracana</i> subsp. <i>africana</i>	USDA, PI315700	Pretoria, South Africa	36
<i>E. indica</i>	USDA, PI231130	Nilgiri Hills, India	18
<i>E. tristachya</i>	KH2414	Uruguay	18
<i>E. multiflora</i>	KH258	Rift Valley, Kenya	16
<i>E. jaegeri</i>	KH221	Narok, Kenya	20
<i>E. floccifolia</i>	USDA, PI196853	Addis Ababa, Ethiopia	18
<i>Dactyloctenium aegypticum</i>	Hilu, KH263	Eldorat, Kenya	—

Phylogenetic relationships among the perennial species have not been examined.

The objectives of this chloroplast DNA study are to elucidate the phylogenetic relationships among species of *Eleusine*, evaluate the proposed infrageneric grouping of the species, provide information on the origin of the New World species *E. tristachya*, assess the affinity of *E. multiflora* to *Eleusine*, and provide additional insight into the origin of polyploid *E. coracana*.

MATERIALS AND METHODS

Chloroplast DNA (cpDNA) was isolated from plants grown in the greenhouse. The species, seed collections, and sources of material for *Eleusine* and the outgroup *Dactyloctenium aegypticum* (L.) P. Beauv. are listed in Table 1. *Dactyloctenium* Willd. and *Eleusine* are members of the subtribe Eleusineinae and are considered to be taxonomically linked (Clayton & Renvoize, 1986). Plant material for *E. intermedia* S. M. Phillips and *E. kigeziensis* S. M. Phillips was not available. A previous study on the cpDNA variation in *Eleusine* (Hilu, 1988) demonstrated the lack of infraspecific variability; thus one collection per taxon was used here.

Seeds were grown in flats and leaves were harvested from 5–7-inch seedlings, frozen in liquid nitrogen, and stored at -70°C . DNA was isolated following the procedure of Saltz and Beckman (1981) as modified in Hilu (1988). The DNA was digested with the restriction endonucleases *Ava*I, *Ava*II, *Bam*HI, *Bcl*I, *Bgl*II, *Dra*I, *Eco*RI, *Ssp*I, *Pst*I. The DNA fragments were resolved electrophoretically on 0.8% agarose gels, stained in ethidium bromide, and photographed in UV light. For the Southern hybridization, DNA was transferred to Zetaprobe nylon membranes (BioRad Inc.) using the alkaline

procedure (Reed & Mann, 1985). The membranes were baked in an oven at 65°C for 2 hours and stored at 4°C .

To examine the restriction sites in the cpDNA, ten *Pst*I cloned cpDNA fragments of barley (provided by T. H. N. Ellis and A. Day) covering 98% of the genome (Day & Ellis, 1985) were used sequentially as hybridization probes. The probes were labeled with ^{32}P using the nick translation kit of Bethesda Research Laboratories Inc. (BRL). The membranes were prehybridized overnight at 65°C in $3\times$ SSC, 20 mM phosphate buffer pH 7.0, 7% SDS, $10\times$ Denhardt's solution, and 100 mg/ml salmon sperm DNA. Identical conditions were used for probe hybridization. Membranes were exposed to Kodak XAR-5 film to visualize homologous bands. Probe stripping was carried on after each hybridization by washing the membranes three times, 20 min. each, in $0.1\times$ SSC and 0.5% SDS at 95°C . DNA fragment sizes were calculated by comparison to Lambda *Hind*III and a 1-kilobase fragment ladder marker (BRL).

Phylogenetically informative sites (i.e., those found in two or more but not all species) were scored as present-absent. Small deletions and additions unique to particular taxa were excluded from the analysis. The data were polarized in relation to the outgroup species *Dactyloctenium aegypticum*, transformed into NEXUS format using MacClade 3.0 (Maddison & Maddison, 1992), and analyzed by the Wagner parsimony method in PAUP version 3.0 (Swofford, 1990). The parsimony analyses were conducted using the exhaustive search method with MULPARS, TBR branch swapping, and CLOSEST addition to estimate relationships and tree topology. The bootstrap method with 100 replications and the branch-and-bound search,

Table 2. Restriction site mutations detected in the cpDNA of *Eleusine* species. The position of the restriction site on the chloroplast genome is identified by the probe used (P1–P7) and the restriction enzyme (see Day & Ellis, 1985, for probes map). When more than one restriction site is revealed by a probe, the sites are designated by an alphabetical letter.

	<i>Eco</i> RI		<i>Ssp</i> I			<i>Bam</i> HI				<i>Ava</i> I		<i>Ava</i> II			<i>Dra</i> I	
	P1	P2	P3a	P3b	P4	P1	P4a	P4b	P7b	P1	P2	P1a	P1b	P5	P1	P2
<i>coracana</i>	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0
<i>indica</i>	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0
<i>tristachya</i>	1	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0
<i>multiflora</i>	0	1	1	0	1	0	1	1	0	1	1	0	1	1	1	1
<i>jaegeri</i>	0	1	1	1	0	1	1	0	0	1	1	1	0	0	1	1
<i>floccifolia</i>	0	1	0	0	1	1	1	0	1	1	1	1	1	1	0	0
<i>Dactyloctenium</i>	0	1	0	1	1	0	1	1	1	1	1	0	0	0	0	1

and the decay analysis were performed in PAUP to determine relative support for the clades (Felsenstein, 1985; Bremer, 1988).

RESULTS

Hybridization of the cpDNA clones to the restriction digests of the *Eleusine* species revealed 28 restriction sites. Sixteen sites were phylogenetically informative, while the remaining 12 were present in only one species (Table 2). Ten of the unique sites were characteristic of the *E. multiflora* genome, one was found in *E. floccifolia* (Forssk.) Spreng., and the other occurred in *Dactyloctenium aegyptium*. Among the cpDNA clones used, P8 did not resolve informative or unique sites. This clone covers the inverted repeat region of the chloroplast genome, a region less likely to produce informative sites because of its highly conserved nature. Small addition-deletions were also observed. The exhaustive search evaluated 945 trees of 23 to 39 steps in length and retained a single, most parsimonious tree of 23 steps. The consistency index (CI) and retention index (RI) for the most parsimonious tree were 0.70, reflecting the relatively low homoplasy on the tree. The bootstrap and the decay index values for the different clades are given in Figure 1.

DISCUSSION

EVOLUTION OF THE *E. CORACANA*–*E. INDICA*–*E. TRISTACHYA* COMPLEX

1. Evolution of Tetraploid Species

The evolution of the tetraploid *E. coracana* subsp. *coracana* and subsp. *africana* and its genomic relationship to the diploid *E. indica* has been the focus of various studies (see introduction). This cpDNA study did not resolve restriction site differences between the two subspecies of *E. coracana*. A similar finding was also obtained in a previous

cpDNA study (Hilu, 1988) that focused on the two subspecies of *E. coracana*, *E. indica*, and *E. tristachya*. These studies thus provide evidence in support of the direct origin of finger millet (*E. coracana* subsp. *coracana*) from *E. coracana* subsp. *africana*. Additional evidence in support of this theory comes from restriction fragment variation in the intergenic spacer region (IGS) between the 17S and 25S ribosomal genes (rDNA). Hilu and Johnson (1992) showed that the domesticated subspecies is quite homogeneous in IGS pattern and that its rDNA phenotype is identical to one of the IGS phenotypes detected in subspecies *africana*. In contrast, recent isozyme data (Werth et al., 1994) demonstrated the presence of alleles in domesticated finger millet, subspecies *coracana*, which were not shared with the proposed wild ancestor subspecies *africana*. Consequently, the study questioned the possibility of a direct origin of subspecies *coracana* from subspecies *africana*. This disagreement has two possible explanations. One, the two tetraploid taxa had different origins, sharing only one common diploid genome; the donor of the second genome might have contributed the unique alleles reported in subspecies *coracana*. This hypothesis is inconsistent with cytogenetical information (Chennaveeraiyah & Hiremath, 1974; Hiremath & Salimath, 1992) that demonstrated complete genome homology between the two taxa. Two, the tetraploid subspecies *africana* is genetically quite variable due to high diversity incurred by polyploidization and possible multiple origin, and subspecies *coracana* was derived from a limited number of populations of subspecies *africana*, a situation typical of crops. Variability in subspecies *africana* was demonstrated in the ribosomal interspacer region (Hilu & Johnson, 1992), isozyme alleles (Werth et al., 1994), and in random amplified polymorphic DNA (RAPD) markers (Hilu, 1995). The rDNA and RAPD studies demonstrated that the DNA patterns

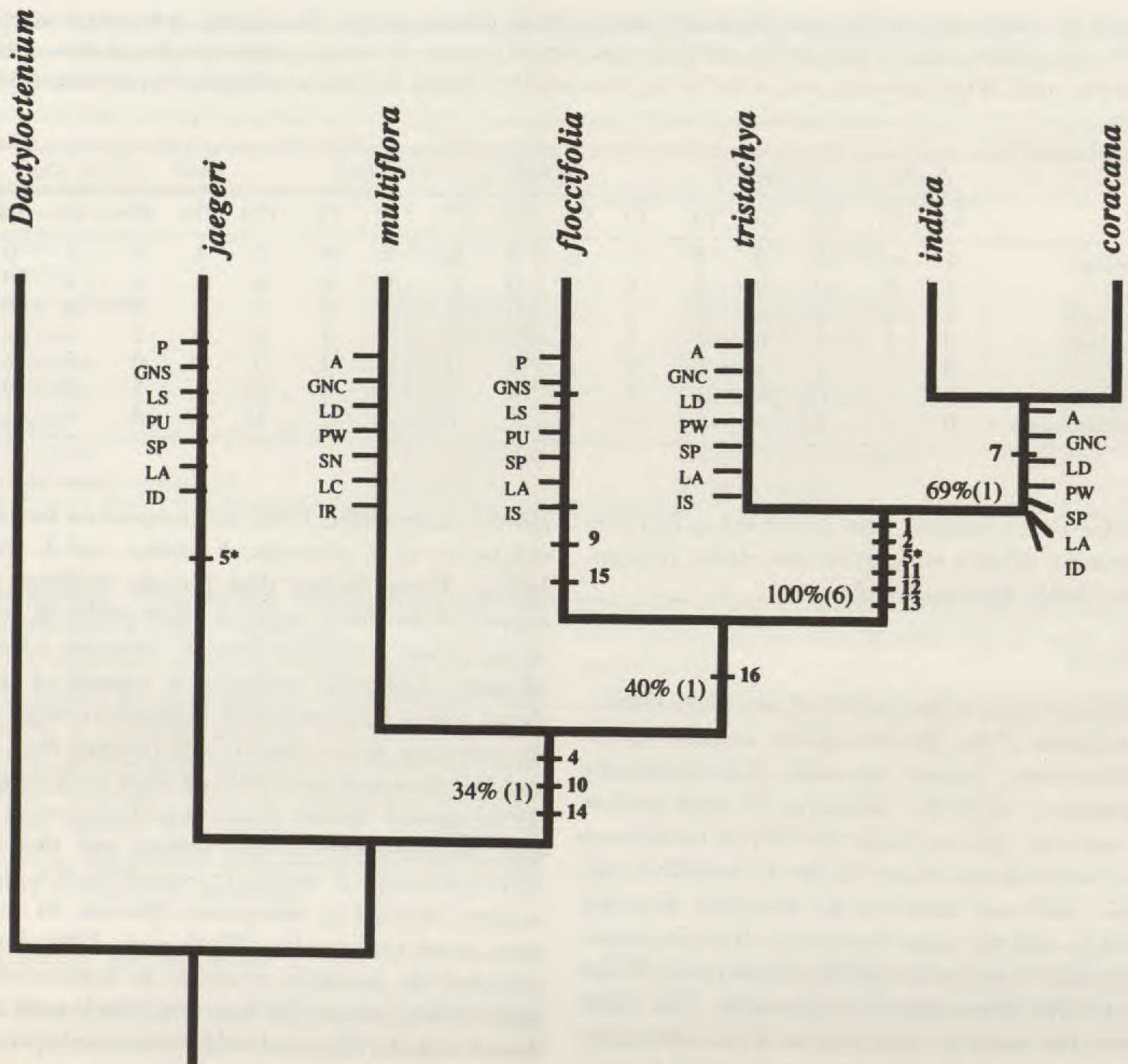


Figure 1. The single most parsimonious tree for the *Eleusine* species rooted with *Dactyloctenium aegyptium* and based on 16 phylogenetically informative cpDNA restriction sites. The two subspecies of *E. coracana* are lumped together since they are identical in restriction sites. The tree was generated through heuristic search with MULPARS, TBR branch swapping, and Simple addition. Numbers on the branches indicate unambiguous apomorphic restriction sites; homoplasy is denoted by an asterisk. Bootstrap support is indicated as percentages based on 100 bootstrap replications, while number of additional steps required to collapse each branch (decay index) is noted in parentheses. The habit and six morphological characters pertaining to the inflorescence, flower, and caryopsis are mapped on the cladogram: A, annual; P, perennial; GNS, glume nerve simple; GNC, glume nerve compound; LS, lemma simple; LC, lemma cuspidate; PW, palea winged; PU, palea unwinged; SP, seed surrounded by pericarp; SN, seed naked (i.e., seed free of pericarp); ID, inflorescence digitate; IS, inflorescence subdigitate-racemose.

(phenotypes) of subspecies *coracana* are present in and can be derived from those of subspecies *africana*, and that these phenotypes represent only a subset of the genetic variation in that tetraploid wild taxon. Due to the demonstrated genetic variability in subspecies *africana*, the isozyme data might represent only part of that variation. Therefore, the origin of the domesticated taxon from one or a few genotypes of the wild tetraploid is a more likely explanation for the incomplete concordance between the isozyme data and the other molecular

information. This explanation is strongly supported by the genomic homology and interfertility between the two taxa (Hiremath & Salimath, 1992). A more extensive isozyme study that includes a large sample of subspecies *africana* from across its range of distribution might shed some light on this disagreement.

Eleusine indica shares the same restriction sites with the two tetraploid subspecies of *E. coracana*, indicating the presence of a common chloroplast genome among the three. This study thus further

supports a previous cpDNA investigation (Hilu, 1988) that pointed to *E. indica* as the "A" genome donor of the tetraploid *E. coracana*. Originally, the diploid species *E. indica* was considered as the genomic donor of finger millet (Greenway, 1945; Kennedy-O'Byrne, 1957; Jameson, 1970). Based on lack of chromosome pairing in a synthetic hybrid between *E. coracana* subsp. *coracana* and *E. indica*, Chennaveeraiah and Hiremath (1974) concluded that the latter species did not contribute any of the genomes of finger millet. That study, however, was based on a single interspecific hybrid. In a more recent cytogenetic study based on more than one hybrid, Hiremath and Salimath (1992) found an appreciable amount of chromosome pairing between the *E. coracana* subsp. *coracana* and *E. indica* genomes, confirming the genomic contribution of *E. indica* to the tetraploid *E. coracana* as proposed by the cpDNA study (Hilu, 1988).

2. Origin of *E. tristachya*

To address the question of the origin and dispersal of the vicariant *Eleusine tristachya*, three points have to be considered. First, the monophyly of *E. tristachya* and *E. coracana* and *E. indica* is substantiated by information from this study (100% bootstrap, decay index of 6, and five unambiguous mutations) as well as from previous molecular, biochemical, and cytogenetic work (Hilu et al., 1978; Hilu & Johnson, 1992; Hiremath & Salimath, 1992; Werth et al., 1994). Second, all the other species of *Eleusine* are native to East Africa and are widely distributed in that region, even when they are found on other continents. Third, *E. tristachya* has relict populations in the Sudan area of Africa. Considering these points, a South American origin of *E. tristachya* is not likely. The species, at its incipient stages of differentiation from the common ancestor of the annuals (species in the terminal clade, Fig. 1), must have moved to South America during the early stages of continental drift. Clayton's (1981) study of the geographic distributions of grass genera promoted the possibility of a Tertiary spread of grass genera across the Atlantic when the latter was a relatively narrow water passage. Dispersal during the post-Columbus trading times is less likely because of the very limited distribution of *E. tristachya* in northeastern Africa.

INTRAGENERIC SYSTEMATIC RELATIONSHIPS

In her revision of the African species of *Eleusine*, Phillips (1972) asserted that the genus can be divided into two groups of species on the basis of the annual and perennial habit. She indicated that

within each group, the differences between species are often small, and that among the annuals in particular, introgression is frequent. In addition to the annual and perennial habit, Phillips cited differences among the two groups of species in spikelet morphology, such as the number of nerves and the presence of a keel in the glumes and lemma, and in the presence of a keel in the palea. These morphological characters are mapped on the cpDNA cladogram (Fig. 1). On the basis of inflorescence and spikelet characters, the annual *E. multiflora* occupies an isolated position in relation to the annual species and the genus as a whole. Its raceme-like inflorescence is atypical of the digitate-spike arrangement in *Eleusine*. Phillips (1972) also noted that *E. multiflora* can be distinguished from the other African species of *Eleusine* by the short, broad spikes. The lemma keel of *E. multiflora* extends into a cusp or a mucro, unlike other species of *Eleusine* where the keel does not extend at the lemma tip. The seed of *E. multiflora* ruptures from the membranous pericarp before it is dispersed from the spikelet, whereas in the other species the seed remains enclosed in the pericarp after dispersal.

The most parsimonious tree based on the cpDNA data showed the three annual species *Eleusine coracana*, *E. indica*, and *E. tristachya* as a terminal lineage strongly supported by six unambiguous restriction sites, a decay index of 6, and 100% bootstrap value (Fig. 1). The fourth annual species, *E. multiflora*, appeared in an individual clade situated between the two perennial taxa. Among the perennials, *E. floccifolia* emerged as a sister species to the annual species assemblage of *E. coracana*, *E. indica*, and *E. tristachya*. The *E. floccifolia* clade was supported by 40% bootstrap and one unambiguous restriction site mutation. The other perennial, *E. jaegeri*, formed a basal clade in the genus, diverging after the outgroup *Dactyloctenium aegyptium*. The position of the *E. floccifolia* clade as a sister taxon to the three annual species receives support from chromosome number and meiotic chromosome behavior (Chennaveeraiah & Hiremath, 1973; Hiremath & Salimath, 1992). These three annual species and *E. floccifolia* are diploids or polyploids based on $x = 9$, in contrast with the basic number of $x = 10$ for *E. jaegeri* and $x = 8$ for *E. multiflora*. Crosses between *E. floccifolia* and the annuals *E. tristachya* and *E. coracana* subsp. *coracana* revealed a good amount of genome homology, with a mean of 7.6 to 8.6 bivalents (Chennaveeraiah & Hiremath, 1973; Hiremath & Salimath, 1992). The high affinity between *E. floccifolia* and the three annual species was also demonstrated

in the isozyme study of Werth et al. (1994). The basal position of *E. jaegeri* in *Eleusine* was previously demonstrated on the basis of isozyme information (Werth et al., 1994). The chromosome numbers for the two other perennials *E. intermedia* and *E. kigeziensis* were reported to be $2n = 18$ and 38, respectively (Hiremath & Salimath, 1991). The $2n = 18$ is indicative of the diploid nature and a basic number of $x = 9$ for *E. intermedia*, a species that appears to be morphologically intermediate between the perennial *E. jaegeri* and the annual complex of *E. coracana*–*E. indica* (Phillips, 1972). The phylogenetic arrangement of the *Eleusine* species could point to a descending order of aneuploid chromosomal evolution from $x = 10$ to both $x = 9$ in the annual species *E. coracana*, *E. indica*, and *E. tristachya* and the perennial *E. intermedia*, and $x = 8$ in *E. multiflora*. The chromosome count of $2n = 38$ for *E. kigeziensis* needs to be verified since it appears as an aneutetraploid when compared with the basic numbers $x = 8, 9,$ and 10 found in *Eleusine*. Hiremath and Salimath (1982) proposed that $x = 9$ not $x = 10$ as the primitive number in *Eleusine*, from which other basic numbers were derived.

This cpDNA study unequivocally supports the monophyly of the three annual species *Eleusine coracana*, *E. indica*, and *E. tristachya* (Fig. 1). It also substantiates the placement of the annual *E. multiflora* within the genus with three unambiguous mutations, but in a lineage distinct from the clade of the other annuals. Consequently, the results indicate that the annual condition appears to have arisen twice in *Eleusine*. The perennial species did not emerge as a monophyletic group. The internal placement of *E. multiflora* among the perennials is probably due to the exclusion from the analysis of the 10 mutations that are unique to this species. When the decay analysis was performed, the three basal clades representing the two perennials and *E. multiflora* in the most parsimonious tree collapsed into a polytomy with one additional step. Forcing *E. jaegeri* and *E. floccifolia* into a monophyletic clade with the Constraint option, the new tree was only two steps longer and the CI index slightly lower (0.64 vs. 0.70). It is to be noted that the basal branch that represents the perennial *E. jaegeri* is supported by only one, homoplastic apomorphy (Fig. 1). These analyses show low support for the basal nodes and imply a weak resolution at the base of the tree.

Further information on the systematics of *Eleusine* comes from previous biochemical, molecular, morphological, and cytogenetical studies. Hilu et al. (1978) surveyed flavonoid variation in the four

annual species of *Eleusine*, the perennial *E. floccifolia*, and *Ochthochloa compressa* (Forssk.) Hilu (a taxon closely allied to *Eleusine*). Although the study could not be used to draw a conclusion concerning the perennials since only one species was represented, it highlighted the similarities among the annuals and underscored a closer affinity of *E. multiflora* to *Eleusine* than to *Ochthochloa*. *Eleusine multiflora* shared three flavonoids common to all other *Eleusine* species but lacking in *O. compressa*. The isozyme study of Werth et al. (1994) substantiated the genetic similarities among the annual species as a group and confirmed the taxonomic affinities of *E. multiflora* to *Eleusine*. Information from restriction site variation in the ribosomal intergenic spacer region (IGS) of six species of *Eleusine* revealed a similar pattern of affinities (Hilu & Johnson, 1992). The study showed the annuals, except for *E. multiflora*, to share similar IGS restriction sites. *Eleusine multiflora* had distinct IGS restriction sites, but displayed phenotypes that are found in *Eleusine*. The perennials *E. jaegeri* Pilger and *E. floccifolia* differed in restriction sites but had comparable IGS variants.

In a phenetic study based on 37 vegetative and reproductive morphological characters of *Eleusine* species and one species each of related *Dactyloctenium* and *Ochthochloa*, Hilu and deWet (1976a) showed the segregation of the annuals (except for *E. tristachya* and *E. multiflora*) in a distinct cluster linked at a correlation coefficient value of about 0.54. The two subspecies of *E. coracana* and *E. indica* formed a tight cluster. *Eleusine tristachya* formed a cluster with *Ochthochloa compressa*. All five perennial species formed one well-defined group with two subgroups; one included *E. intermedia* and *E. semisterilis*, whereas the other contained *E. floccifolia*, *E. kigeziensis*, and *E. jaegeri*. *Eleusine multiflora* formed a group with *D. aegyptium* that was last to cluster with the *Eleusine* species. Therefore, the morphological study confirms the taxonomic affinities among the perennial species and underscores the distinct position of *E. multiflora*. The spikelet morphology of the annual *E. tristachya* has possibly led to the separation of this species from the remaining annuals.

It is evident from the cpDNA and the above studies that the annual species *Eleusine coracana*, *E. indica*, and *E. tristachya* represent a monophyletic group of closely related species and that the remaining annual *E. multiflora* is a morphologically and genetically distinct taxonomic entity in the genus. The raceme-type inflorescence of this species in a predominantly digitate-type genus could raise the question of whether *E. multiflora* is a member

of *Eleusine*. The inflorescence of *E. tristachya* and some collections of *E. coracana* subsp. *africana* show a tendency toward the raceme-type (Hilu & deWet, 1976b). Removing *E. multiflora* from *Eleusine* will only create another monotypic genus, as the species would not fit well in other related genera. The taxonomic treatment of the perennial species remains problematic. None of the morphological treatments is phylogenetically based and, thus, it is difficult to compare them with the cpDNA results. Available evidence, therefore, points to a possible paraphyletic origin of these taxa from an ancestral stock of *Eleusine*, as the monophyly of the genus is well demonstrated in this investigation.

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THE FRUITS OF *JASMINUM MESNYI* (OLEACEAE), AND THE DISTINCTION BETWEEN *JASMINUM* AND *MENODORA*¹

Jens G. Rohwer²

ABSTRACT

The fruit and seed morphology and anatomy of *Jasminum mesnyi* are described here for the first time, as part of a larger comparative study on the fruit and seed structures in the Oleaceae. The evidence presented here weakens the current delimitation between *Jasminum* and *Menodora*. As usual in *Jasminum*, the two carpels of the ovary of *J. mesnyi* grow up independently to form separate mericarps, while the septum remains small. At maturity, however, the mericarps dry out and dehisce loculicidally on their adaxial side, from the style outward. The wall of the mericarps is membranous at their distal ends, but increasingly thickened toward the base. This is unique in *Jasminum* but reminiscent of *Menodora*, where the mericarps of most species show circumscissile dehiscence. The seed coat of *Jasminum mesnyi* is as unequal-sided as in *Jasminum nudiflorum*, which in turn shares dry, irregularly fragmenting mericarps with *Menodora spinescens*. After a discussion of the characters supposed to separate the two genera, it is concluded that the discontinuity between them is not greater than among some of the sections of *Jasminum*. A decision on the final status of these taxa is deferred until detailed molecular evidence becomes available.

Jasminum is by far the largest genus within the Oleaceae, although recent estimates as to its number of species differ widely, from ca. 200 (Green, 1994) to ca. 450 (Mabberley, 1987). The vast majority of the species have white flowers and opposite leaves, whereas the eight species of section *Alternifolia* DC. (Green, 1961) are characterized by yellow flowers and alternate leaves. Only two species, *Jasminum nudiflorum* Lindl. and *J. mesnyi* Hance, combine yellow flowers with opposite leaves. The fruit of *Jasminum* is usually described as a double berry, which arises through independent growth of the two carpels of the ovary, while the septum grows much in thickness but very little in extent. In earlier papers (Rohwer, 1993, 1994, 1995b) it was shown that the fleshy part of the fruit originates from the seed coat rather than the pericarp, and that the seed structure allows one to distinguish the sections of the genus. *Jasminum nudiflorum* turned out to be unusual in that its fruit does not become black at maturity but rather dries out and fragments irregularly, releasing the seeds. The fruit of the closely related *Jasminum mesnyi*, however, remained unknown, even though the species is frequently cultivated as an ornamental. Fletcher (1916) reported that "*J. primulinum* Hemsl.," as the species is usually called in the horticultural trade, had to be introduced to England as whole

plants, because the plant collector E. H. Wilson, working for Veitch's nurseries, had searched in vain for seeds. Fletcher claimed that he had obtained a few seeds of *J. mesnyi* from pollination with both its own pollen and that of *J. nudiflorum*, but gave no details about the fruit. Otherwise, the species has obviously been propagated only vegetatively so far. Green (1965) commented on the apparent sterility of the cultivated plants, citing different chromosome counts ($2n = 24, 26, 39$) and suggesting that at least some clones were triploid.

MATERIALS AND METHODS

In the botanic garden of Heidelberg, attempts to achieve fruit-set in *Jasminum mesnyi* by artificial pollination (either geitonogamously, since all plants within reach were from the same clone, or with pollen from *J. nudiflorum*) failed for several years. Only after these attempts had been abandoned were four young fruits found in April 1996. One of them was fixed in FAA (5 ml formalin, 5 ml glacial acetic acid, 56 ml ethanol 96%, aqua dest. ad 100 ml) on May 24, at an obviously immature stage. The other three were bagged in nylon nets, as a precaution against loss due to premature abortion, with the hope that at least one of them would develop until maturity. The bags were inspected at intervals of

¹ I thank P. S. Green (Kew) for providing literature unavailable in Germany. S. Ball stained and mounted the sections, and U. Wagenfeld processed the photos.

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two to three days. The fruits slowly became larger and paler, but did not look quite mature even on June 17. On June 19 they were found open, with the seeds still attached in one of them but shed into the bag in the others. All available material was fixed in FAA. A flowering voucher specimen (Rohwer 135) of the investigated plant had been deposited in HEID earlier.

For sectioning, the material was transferred to 70% ethanol for at least a day, then embedded in a 2-hydroxy-ethyl methacrylate resin (Kulzer's Technovit 7100; for details, see Igersheim, 1993), sectioned with a rotary microtome (Leica RM 2145) at a thickness of 3–6 μm , stained with Giemsa solution for 2 hr. (2.5 ml Gurr's improved R66 in 100 ml aqua dest.), differentiated in aqua dest. with two or three drops of acetic acid and subsequently in 96% ethanol, each for about 5–20 sec. according to the intensity of the stain, transferred to xylene via isopropanol, and enclosed in Vitro-Clud embedding medium. The microphotos were taken with a Zeiss Axioskop on Agfapan APX 25 film.

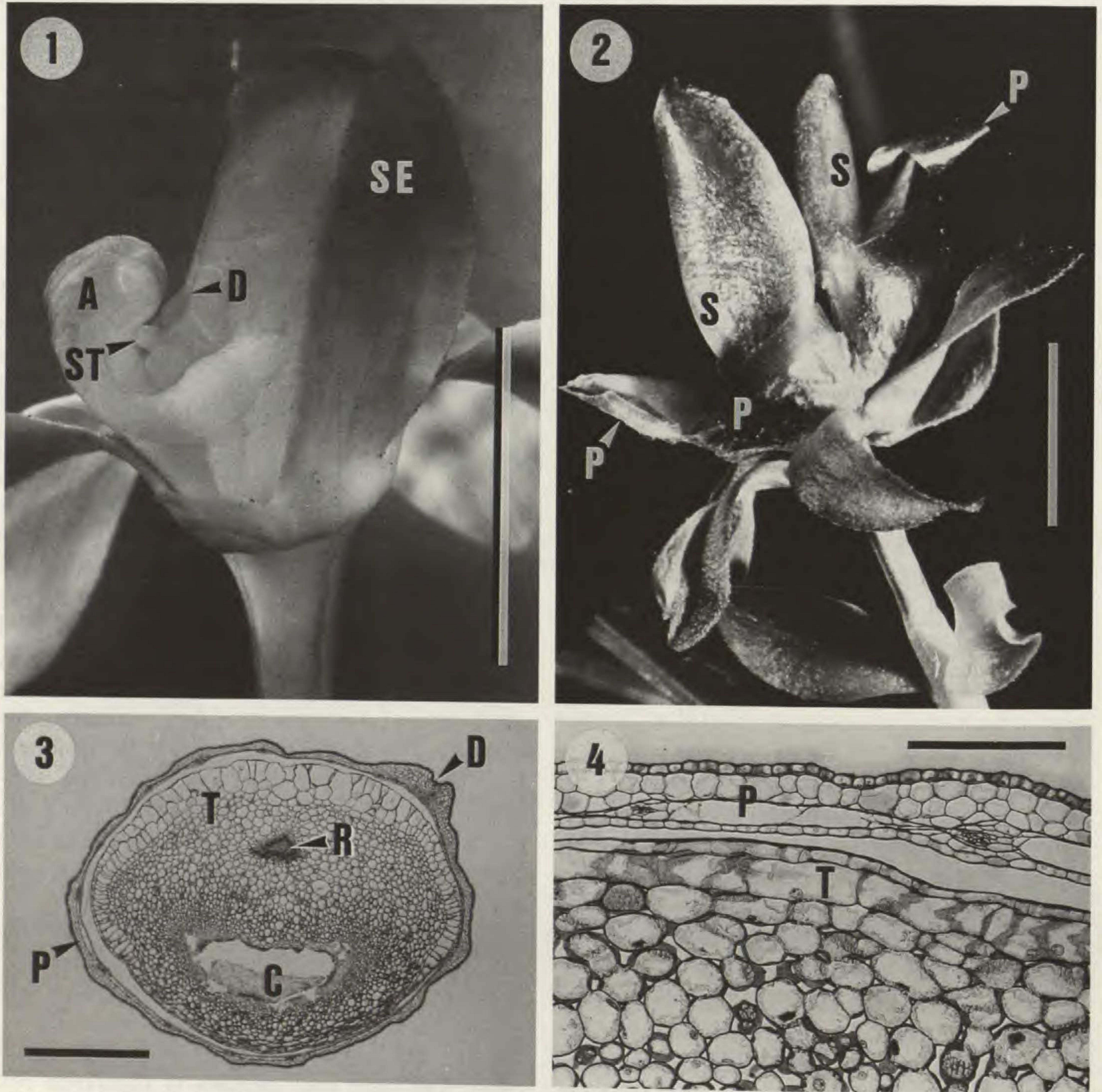
RESULTS

In the young fruit of *Jasminum mesnyi* (Fig. 1), it is obvious that both carpels of the ovary had started to grow up to form separate mericarps. In all four fruits, however, one of the two mericarps ended its development early, while the other continued to grow. In this case the developing mericarp shifts to a position almost in continuation of the pedicel, displacing the aborted mericarp and the remnant of the style sideways. Early on, a longitudinal ridge with a shallow furrow in its middle becomes visible close to the style (Fig. 1), becoming more and more distinct and stretching more toward the distal end of the developing mericarp with maturity. At maturity, not only the fertile mericarp but the whole fruit opens along this suture, splitting the style in half (Fig. 2). In one of the three mature fruits the dehiscence continued in a straight line along the carpel median, over the tip down to the base of the fertile mericarp. In the other two the splitting was straight only slightly beyond the point where the suture becomes indistinct, followed by an irregular, branched crack above.

In the immature fruit (Figs. 3, 4), the pericarp consists of an outer epidermis of small, isodiametric to slightly flattened cells with a rather thick cuticle, several at least initially parenchymatous layers, and an inner epidermis of small, thin-walled, slightly flattened cells. Numerous small, weakly developed vascular bundles are found embedded among the inner parenchyma-

tous layers. These layers, about four to six in the distal part of the mericarp, cannot keep up with the growth of the fruit in the areas between the vascular bundles, so that they are destroyed early in fruit development. The outer epidermis, some outer parenchymatous layers (one or two distally, more toward the base), and the inner epidermis remain distinct for most of the fruit development. At maturity, only the outer epidermis and its hypodermal layer are still recognizable in the distal part of the mericarp (Figs. 5, 6). Slightly below the tip, the fruit wall becomes thicker on both sides of the dehiscence line, and polygonal cells with slightly thickened, pitted, lignified walls appear (Fig. 7). The most distal ones of them are more or less isolated, but soon they aggregate to form woody strands along the suture. Further toward the base, these strands not only become thicker but also extend further around the mericarp (Fig. 8). Even at the base, however, there are about as many parenchymatous as sclerified cells in the abaxial wall of the mericarp (Figs. 9, 10). The outer and the inner epidermis, the (usually no more recognizable) inner parenchymatous layers, and several layers forming the weakness zone within the suture are never lignified. Otherwise, the thickness of the cell walls and the degree of lignification increase from the abaxial side of the mericarp toward the suture, and from the outside inward.

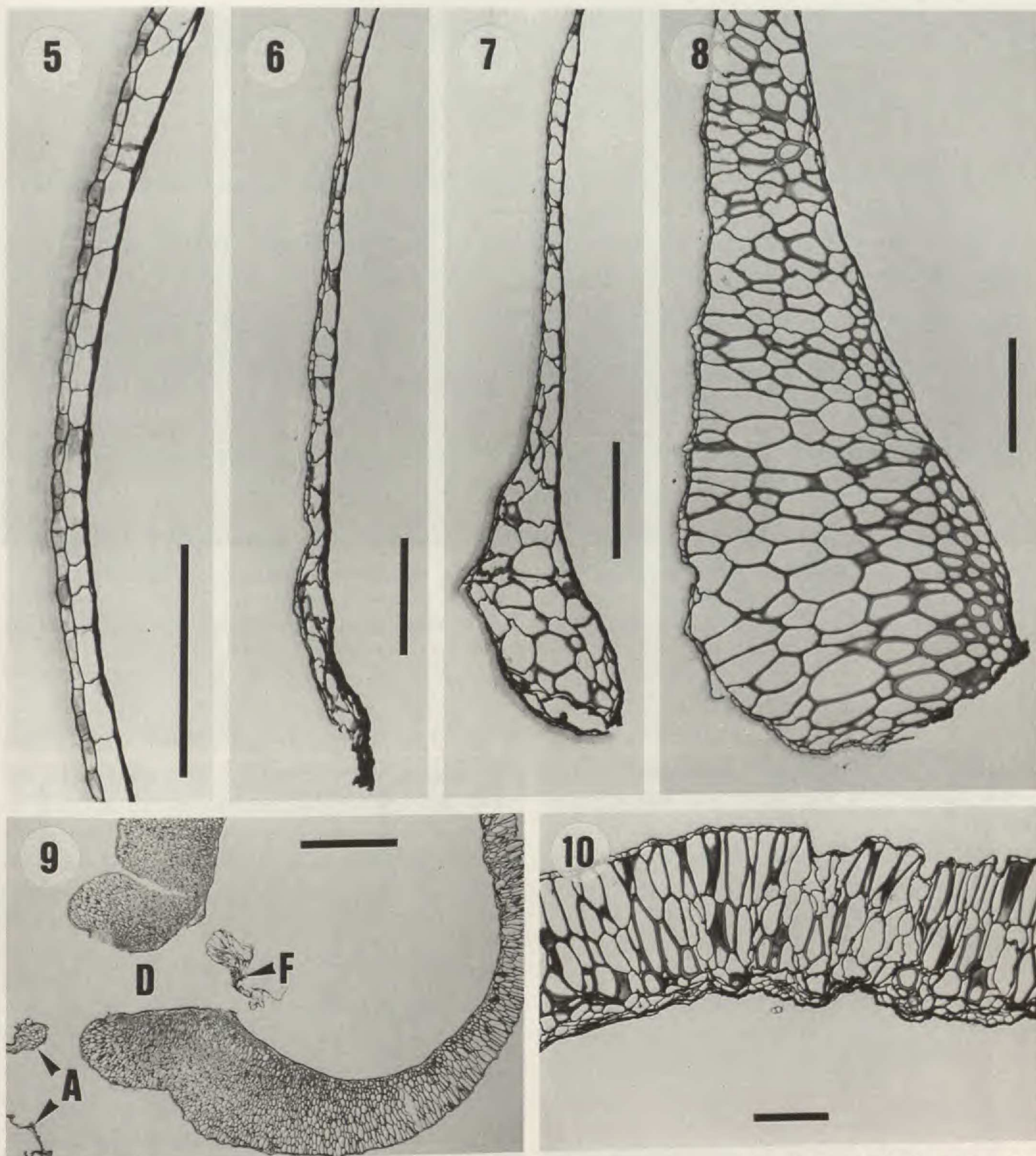
The seeds are elongate, about 8–10 mm long and 3.5–4.5 mm wide. Their outline in cross section (Fig. 11) is thickly plano-convex when both ovules of a locule develop; otherwise it is elliptic. The two seeds face each other with their raphal sides. The seed coat consists of numerous cell layers, of which the inner ones are gradually destroyed by the growing endosperm. As in other species of *Jasminum*, but in contrast to most other Oleaceae, there is no trace of an endothelium (jacket layer) at any time during development. The two outermost layers are very different from the rest of the seed coat, and unequally developed on the two sides of the seed (Figs. 11, 12). On the antiraphal side (Fig. 13), the outer epidermis (exotesta) consists of small, transversely elongate cells with thickened, lignified walls, more massive on the outside than on the inside. The cells of the hypodermal layer are much larger, with massive, lignified thickenings occupying almost their entire anticlinal walls, and much smaller thickenings on the periclinal walls. All further layers are parenchymatous and entirely collapsed at maturity. On the raphal side (Fig. 14), the cells of the exotesta are much larger,



Figures 1-4. Fruits of *Jasminum mesnyi*. —1. Immature fruit, the sepal in front removed. —2. Mature, open fruit with the seeds (S) still attached. —3. Cross section of young fruit, approximately at the middle. —4. Cross section of young pericarp and outer layers of young testa. A = aborted carpel, C = cotyledons, D = dehiscence line, P = pericarp, R = raphe bundle, S = seed, SE = sepal, ST = style, T = immature testa. Scale bars in 1, 2 = 5 mm, in 3 = 1 mm, in 4 = 200 μ m.

forming a palisade of hexagonal cells. The lignified wall thickenings are much weaker and almost entirely restricted to the anticlinal walls, usually to the corner where three cells meet. The cells of the hypodermal layer are longitudinally elongate and smaller than those of the exotesta, though still larger than on the antiraphal side. They have (mostly two) band-shaped wall-thickenings in their anticlinal walls, occasionally also in their outer periclinal wall. When the seed dries out, the two outer layers separate from the rest of the seed coat, tearing apart the thin inner end of the anticlinal cell walls in the hypodermal

layer. In the area where this separation occurs, several of the following cell layers have band-shaped wall thickenings as well, much smaller than in the hypodermal layer and becoming still smaller and more irregularly distributed toward the inside (Fig. 14). Below them follows the raphe bundle, which is the only vascular bundle of the seed, and several parenchymatous layers that are increasingly collapsed toward the inside. About three to five (only apically and basally more) layers of endosperm surround the embryo, which has very large, flat cotyledons with well-developed, usually two-layered palisade paren-



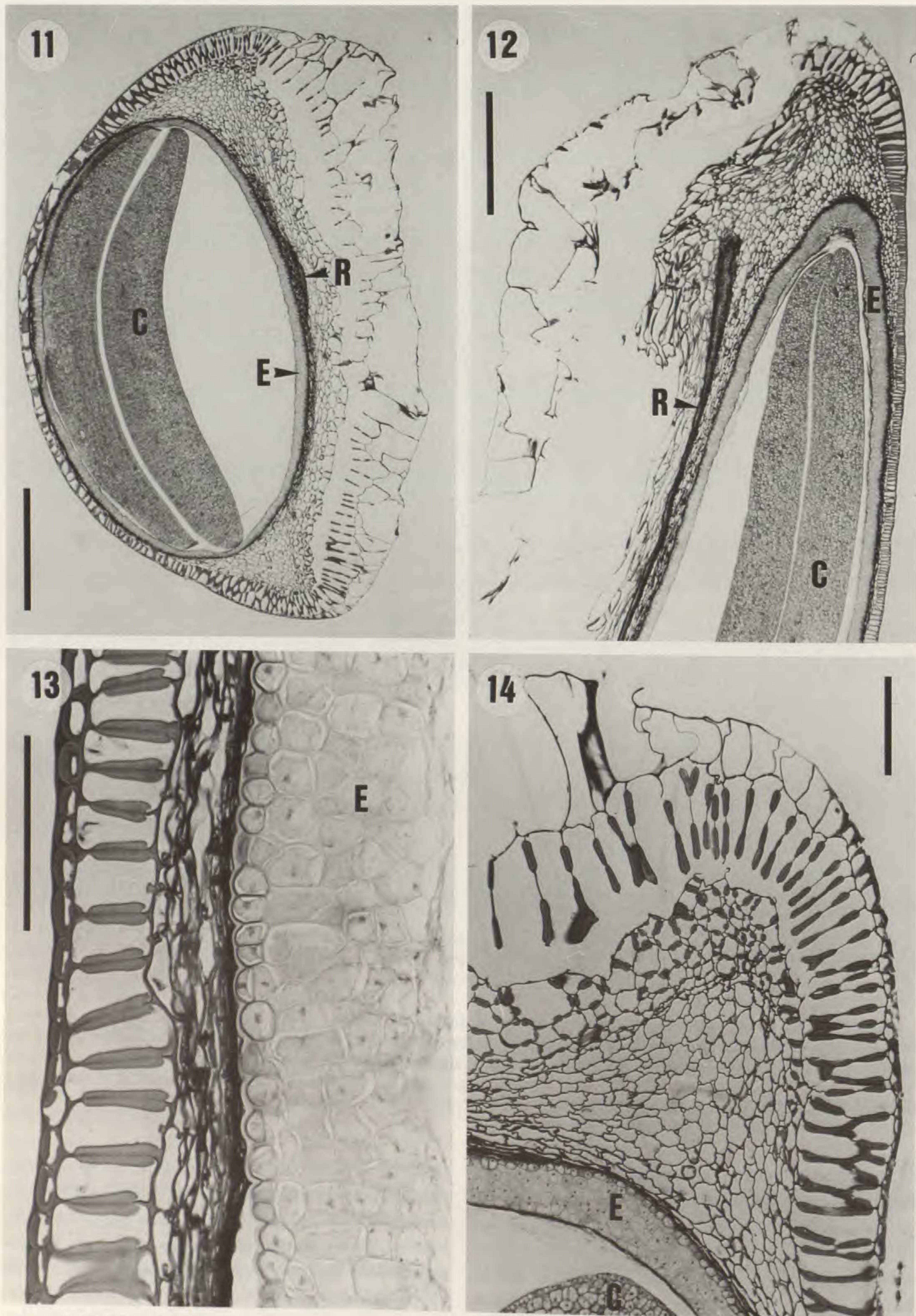
Figures 5–10. Cross sections of mature pericarp of *Jasminum mesnyi*. —5. Membraneous, distal part. —6–8. Pericarp with dehiscence line (bottom), from slightly below the apex of the mericarp (Fig. 6) to slightly below the middle (Fig. 8). —9. Basal part of the fertile mericarp, slightly above the level where the two mericarps become separate. —10. Pericarp on abaxial side, same section as in Figure 9. A = remains of aborted carpel, D = dehiscence line, F = remains of funicular tissue. Scale bars in 5, 6, 7, 8, 10 = 200 μm , in 9 = 1 mm.

chyma. Starch was not found in either the endosperm or the embryo.

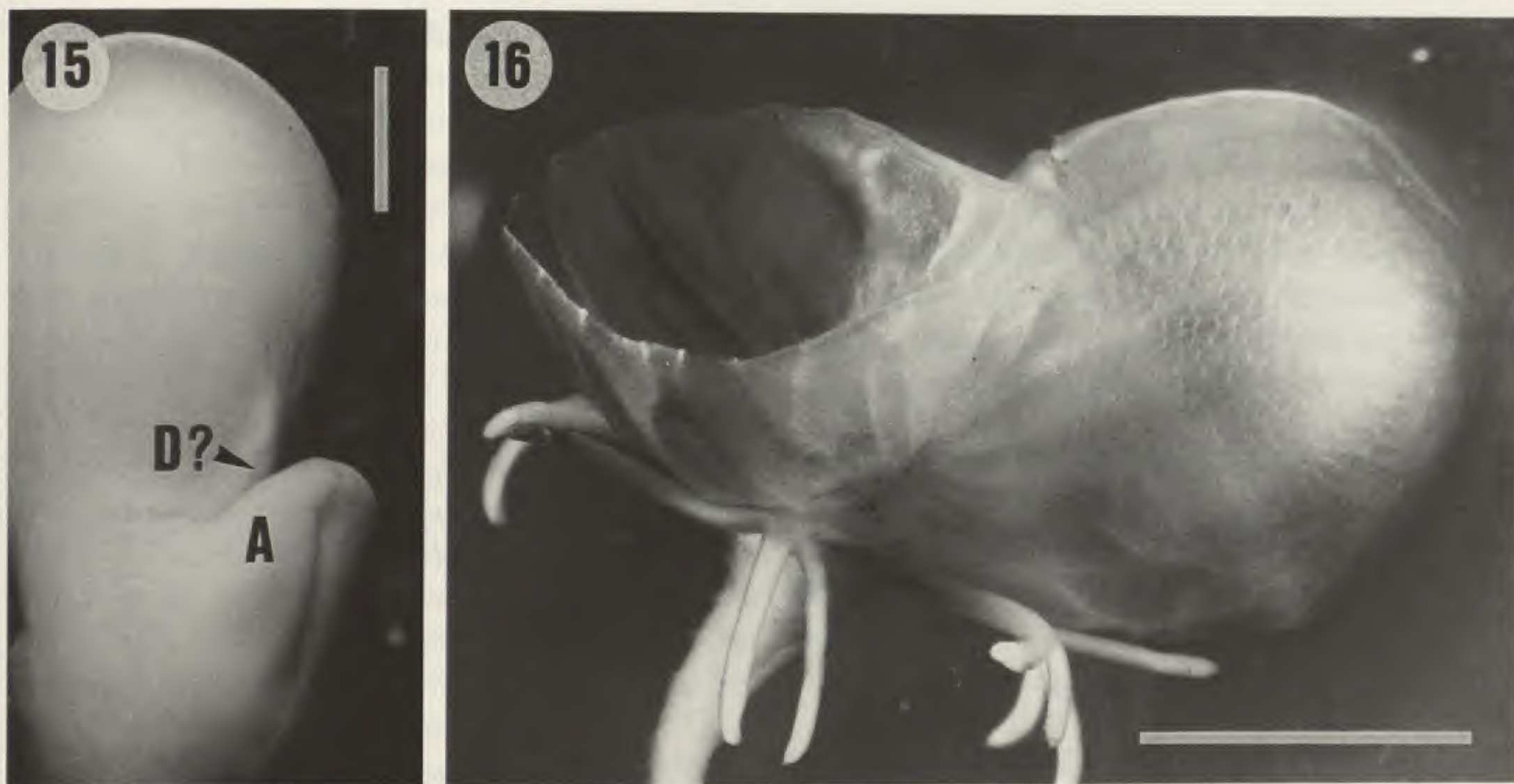
DISCUSSION

The fruit of *Jasminum mesnyi* agrees with that of the other species of *Jasminum* in the development of two separate mericarps. With its loculicidal dehiscence, however, it goes beyond the current circumscription of the genus, which has normally indehiscent fruits with a membranous to coriaceous

pericarp and seeds with a fleshy testa. Dry but irregularly fragmenting fruits, and seeds with an almost identical structure as in *J. mesnyi*, have recently been described in another well-known ornamental species, *J. nudiflorum* (Rohwer, 1993, 1994, 1996). The development of a median suture can even be observed in young fruits of this species (Fig. 15), but none of the open fruits observed so far had actually dehisced along this line. In addition, the pericarp of *J. nudiflorum* is almost ho-



Figures 11-14. Seeds of *Jasminum mesnyi*. —11. Cross section. —12. Longitudinal section, chalazal end. —13. Testa and endosperm on antiraphal side, longitudinal section. —14. Edge of raphal side (above), cross section. C = cotyledon, E = endosperm, R = raphe bundle. Scale bars in 11, 12 = 1 mm, in 13 = 100 μ m, in 14 = 200 μ m.



Figures 15, 16. Comparable fruit structures in other species. —15. *Jasminun nudiflorum*, very young stage of fruit development. —16. *Menodora africana*, mature fruit, the mericarp on the left open and empty, the one on the right still closed, showing the difference between the thicker proximal part and the thinner distal part (hexagonal wall thickenings of the seed coat shining through). A = Aborted mericarp, D? = ridge with longitudinal furrow, similar to the dehiscence line in *J. mesnyi*. Scale bars in 15 = 1 mm, in 16 = 5 mm.

mogeneously membranous throughout, with only a few stone cells near the base, so that it lacks the mechanism for an orderly dehiscence. All other characters, however, whether vegetative, floral, or seed characters, show beyond doubt that the two species are very closely related. Still the differences appear important enough to reject the view expressed by Henry (1904), who thought that "*J. primulinum*" was just a variety of *J. nudiflorum*.

Fruits with dry, dehiscent mericarps are, within the Oleaceae, the most important diagnostic character for *Menodora*, a small genus (22 spp.; Steyermark, 1932; Turner, 1991, 1995) of low shrubs or, more frequently, suffruticose to almost entirely herbaceous plants. In this genus, however, the dehiscence of the fruits is not longitudinally loculicidal but normally circumscissile (Fig. 16). In *M. africana* Hook. at least, where the fruits and seeds have been described in detail recently (Rohwer, 1995a), the pericarp is thicker below the equatorial suture line, but does not contain stone cells, or any other lignified elements, except in the very base of the fruit. No trace of a median suture line was found in this species, at any stage of development.

As an exception within the genus, Steyermark (1932) described the presence of a median suture in *Menodora spinescens* A. Gray, but he never found fruits that had opened along this line. The shape of the fruit is likewise unusual. The mericarps are elongate and spreading in *M. spinescens*, whereas they are subglobose and more or less appressed

against each other in the other species. *Jasminum mesnyi* has similarly elongate mericarps, and this suggests that they would most likely spread if both were developed. In *J. nudiflorum*, in contrast, they are roundish and adjoining. This character seems to be of minor significance, since there are many parallel cases and intermediate forms known from *Jasminum*, often in closely related species (e.g., roundish/adjoining in *J. bignoniaceum* Wall. ex G. Don, intermediate in *J. humile* L., elongate/spreading in *J. odoratissimum* L.). More important is the aberrant number of ovules in *M. spinescens*. While the other species of *Menodora* have four ovules per locule, *M. spinescens* has only two, like most other Oleaceae, including the yellow-flowering species of *Jasminum*, whereas the majority of the white-flowering species of *Jasminum* have only one. This again bridges the discontinuity between the two genera. In *Menodora*, the information given by Steyermark (1932) and Turner (1991) suggests that *M. spinescens* is the only species with basically white flowers (often tinged with brownish purple), whereas the basic flower color of the other species is yellow (sometimes tinged with red to purple).

Inasmuch as the fruits of *Jasminum mesnyi* and *Menodora spinescens* suffice to undermine the traditional distinction between *Jasminum* and *Menodora*, it may be worthwhile to examine other characters that could possibly separate the two genera (summarized in Table 1). Habit (shrubs and climbers in *Jasminum* versus at most subshrubs in *Men-*

Table 1. Distinguishing features of selected taxa of *Jasminum* and *Menodora*.

	<i>Jasminum</i> sect. <i>Jasminum</i>	<i>Jasminum</i> sects <i>Tri- & Unifoliolata</i>	<i>Jasminum</i> sect. <i>Alternifolia</i>	<i>Jasminum</i> <i>nudiflorum</i>	<i>Jasminum</i> <i>mesnyi</i>	<i>Menodora</i> <i>spinescens</i>	<i>Menodora</i> <i>africana</i>	Most <i>Menodora</i> spp.
Habit	climbers	shrubs/climbers ^a	shrubs	shrubs	shrubs	shrubs	herbs	±herbs ^b
Leaf arrangement	opposite	opposite	alternate	opposite	opposite	alternate	opp. or alt.	opposite
Leaves	pinnate	trifol./simple	trifol. or pinn.	trifoliolate	trifoliolate	simple	dissected	simple
Flower color	white	white	yellow	yellow	yellow	whitish	yellow	yellow
Corolla tube/anthers	long/included	long/included	long/included	long/included	long/included	short/exserted	short/exserted	short/exserted ^c
Ovules per locule	usually 2	usually 1	2	2	2	2	4	4
Fruit at maturity	fleshy, black	fleshy, black	fleshy, black	pale, dry	pale, dry	pale, dry	pale, dry	pale, dry
Shape of mericarps	variable	variable	variable	roundish	elongate	elongate	roundish	roundish
Dehiscence of mericarps	—	—	—	irregular	longitudinal	irregular	circumscissile	circumscissile
Median suture	—	—	—	rudimentary	functional	non-functional	—	—
Vascular bundles/seed	1	many	1	1	1	1	1	unknown
Structure of exotesta	sarcotesta	sarcotesta	small-celled	unequal ^d	unequal ^d	not preserved	small, thickened	unknown
Gap within testa	—	—	—	+	+	+	+	unknown
Mesotestal layers with wall thickenings	1	several	several	unequal ^e	unequal ^e	3	3	unknown
Cotyledons	flat or storage	storage	flat	flat	flat	flat	flat	probably flat
Chromosome number 2n	26	26	26	52	24, 26, 39	unknown	unknown	22 ^f

^a *Jasminum siamense* is only suffrutescens.^b *Menodora robusta* is a robust shrub.^c But *Menodora longiflora*, in all other characters a typical *Menodora*, has a long corolla tube with included anthers.^d Small, thick-walled cells on antiraphal side, sarcotesta on raphal side.^e One on antiraphal side, several on raphal side.^f So far only North American species examined.

odora) is rarely used as a diagnostic character (or only as a supplementary character, as by Verdoorn, 1956, 1963), but is frequently mentioned in descriptions. However, *M. robusta* (Benth.) A. Gray and *M. spinescens* are quite robust, erect shrubs, whereas *J. parkeri* Dunn is a prostrate to decumbent shrublet and *J. siamense* Craib is (always?) a weak subshrub, both species not more than 30 cm tall. More frequently used as a diagnostic character is the relative length of the corolla tube and the position of the anthers (e.g., Kupicha, 1983). Corolla tubes that are about as long as the corolla lobes or longer, with included anthers, are characteristic of *Jasminum*, whereas exerted anthers and corolla tubes much shorter than the lobes are supposed to characterize *Menodora*. This character fails, however, in *M. longiflora* (Engelm.) A. Gray, a North American species, which has long corolla tubes and included anthers, but otherwise is typical of *Menodora*. Taylor (1945) and Johnson (1957) use chromosome number ($n = 11$ in *Menodora* vs. $n = 13$ in *Jasminum*) as a supplementary character in the diagnosis of the genera. However, it cannot yet be accepted as proven that this is a real discontinuity. While *Jasminum* appears to have been adequately sampled by now, with counts of $n = 13$ from numerous species belonging to different sections of the genus and coming from different regions of the world, the same cannot be said about *Menodora*. To my knowledge, neither the aberrant *M. spinescens* nor any South American or South African species has been examined so far.

The seed structure of *Jasminum mesnyi* and *J. nudiflorum* differs from that of all other species of both *Jasminum* and *Menodora* so far investigated. In the other species of *Jasminum*, the seeds may be plano-convex in cross section when there are two per locule, but they are never even nearly as unequal-sided as in *J. mesnyi* and *J. nudiflorum*. Our knowledge about seed structure in *Menodora* is still inadequate. Only two species have been examined so far (Rohwer, 1995a), *M. spinescens* and *M. africana*, only the latter in all stages of development. This species has an exotesta of small cells, in which the outer wall becomes so much thickened as to occlude the lumen (almost) completely, even more than on the antiraphal side in *J. mesnyi*. As a consequence of this thickening, which occurs long before maturity in *M. africana*, the exotestal cells can neither enlarge nor divide any further as the seed grows, so that the exotesta becomes discontinuous at maturity. The following layers are similar to those near the edges of the seed in *J. mesnyi*. The hypodermal layer consists of very large cells with conspicuous thickenings in the anticlinal

walls, followed by a few layers of much smaller cells with much smaller, more irregularly distributed thickenings. A gap between the outer two layers and the rest of the seed coat, as on the raphal side in *J. mesnyi*, can even be observed in *M. africana*, all around the seed but more distinct on the antiraphal side. In *M. spinescens*, however, the separation occurs deeper in the seed coat, between the outer layers with thickenings and the inner parenchymatous part. The fate of the exotesta, unfortunately, could not be followed in the relatively poor material available of this species. In any case, the seed of *M. spinescens* appears more similar to that of *M. africana* than to those of any species of *Jasminum*.

In summary, the distinction between *Jasminum* and *Menodora* is not as straightforward as most treatments of the family imply, and the gap is further closed by the data presented here for *J. mesnyi*. Kim and Jansen (1993) found that *Jasminum* and *Menodora* share a 21 kb inversion in the chloroplast genome, and that *Menodora* and some species of *Jasminum* agree in the loss of *clpA* gene introns. This would suggest that *Jasminum* may be paraphyletic with respect to *Menodora*. Unfortunately, their results were published as an abstract only, so that a full comparison with their data is still impossible. A similar conclusion was reached, however, through a detailed study of the fruit and seed structures of the Oleaceae (Rohwer, 1996). With the addition of *J. mesnyi*, it becomes clear that the discontinuity between *Jasminum* and *Menodora* is not greater than the gaps encountered within *Jasminum*, namely among the species with (a) alternate leaves and yellow flowers (sect. *Alternifolia*), (b) opposite leaves and yellow flowers (*J. mesnyi* and *J. nudiflorum*), and (c) opposite leaves and white flowers (sects. *Jasminum*, *Trifoliolata*, and *Unifoliolata*). Demoting *Menodora* to the rank of a section under *Jasminum* would perhaps make the system of the Oleaceae slightly more natural, but this small gain is overcompensated by the danger of losing information on the few species of *Menodora* among the hundreds of *Jasminum*. The most logical alternative solution, i.e., giving generic rank to all four groups, should wait until the details of the molecular analysis become available; it would also require new generic names for groups a and b.

For the morphological interpretation of the relationships within the *Jasminum*-*Menodora* complex, it would be most important to know whether the dehiscent fruits of *J. mesnyi* were a primitive or an advanced feature. Loculicidal dehiscence as such is certainly plesiomorphic within the Oleaceae (Rohwer, 1996), but it is questionable whether this

is true also for *J. mesnyi*. On the one hand it appears unlikely that such a functional character should be at first lost and then secondarily regained within a family, but on the other hand the construction of the mechanical tissue in *J. mesnyi* is entirely different from that in the other Oleaceae. In these we find a sharply delimited endocarp, consisting of fibers that are stretched transversally to diagonally on the flanks of the fruit, but longitudinally along the suture. This pleads clearly in favor of an independent origin. It is tempting to add that it would be difficult to understand how and why three different modes of dehiscence, loculicidal, irregular, and circumscissile, would have evolved within in the *Jasminum*-*Menodora* complex when one of them had already been established. This, however, is a weak argument, because the presence of a non-functional suture in the species with irregular dehiscence (*J. nudiflorum*, *M. spinescens*) shows that such a development must have occurred anyway.

Considering the morphological differences within *Menodora* and the widely disjunct distribution of the genus (southwestern North America, southern South America, and South Africa), it may be asked whether *Menodora* is even monophyletic. For the bulk of the genus, there is little doubt. The combination of herbaceous habit, four ovules per locule, and separate, circumscissile mericarps is too unusual to have arisen more than once. *Menodora spinescens*, however, shows none of these character states, so that its placement within this genus (e.g., as opposed to *Jasminum*) may appear questionable. However, its minute leaves, short corolla tube, exerted anthers, and separate, dry mericarps sharply distinguish it from *Jasminum*, and make it far more similar to the typical *Menodora* species than to any other taxon. In its habit it resembles the more robust species of this genus, especially *M. robusta*. Therefore, it makes little sense to remove *M. spinescens* from the genus, unless it can be shown that it is not the closest sister group to the remaining species. Further studies are needed to elucidate its relationships within this complex.

The unexpected morphological and anatomical data presented here, in a supposedly well-known species, thus raise a number of questions that presently cannot be answered with confidence. The purpose of the present paper is to bring them to notice, for consideration in future studies.

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REVISIÓN DEL GÉNERO
GALIANTHE SUBG. *EBELIA*
STAT. NOV. (RUBIACEAE:
SPERMACOCEAE)¹

Elsa L. Cabral² y Nélica M. Bacigalupo³

RESUMEN

Se subordina al género *Galianthe* (Rubiaceae: Spermaceae) el subgénero *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo, que agrupa las especies que presentan frutos de mericarpos indehiscentes. Se reconocen nueve especies: *Galianthe bogotensis* (Kunth) E. L. Cabral & Bacigalupo, *Galianthe brasiliensis* (Spreng.) E. L. Cabral & Bacigalupo, *Galianthe cymosa* (Cham.) E. L. Cabral & Bacigalupo, *Galianthe dichasia* (Sucre & C. G. Costa) E. L. Cabral, *Galianthe dichotoma* (Willd. ex Roem. & Schult.) E. L. Cabral & Bacigalupo, *Galianthe hispidula* (A. Rich. ex DC.) E. L. Cabral & Bacigalupo, *Galianthe polygonoides* sp. nov., *G. humilis* sp. nov. y *G. vaginata* sp. nov.; las tres últimas viven en Brasil. Todas se describen e ilustran.

ABSTRACT

A new subgenus, *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo, is proposed within the genus *Galianthe* (Rubiaceae: Spermaceae). The species included therein are characterized by their fruits with indehiscent mericarps. Nine species are recognized: *Galianthe bogotensis* (Kunth) E. L. Cabral & Bacigalupo, *Galianthe brasiliensis* (Spreng.) E. L. Cabral & Bacigalupo, *Galianthe cymosa* (Cham.) E. L. Cabral & Bacigalupo, *Galianthe dichasia* (Sucre & C. G. Costa) E. L. Cabral, *Galianthe dichotoma* (Willd. ex Roem. & Schult.) E. L. Cabral & Bacigalupo, *Galianthe hispidula* (A. Rich. ex DC.) E. L. Cabral & Bacigalupo, *Galianthe polygonoides* sp. nov., *G. humilis* sp. nov., and *G. vaginata* sp. nov.; the last three are found in Brazil. All the species are described and illustrated.

La delimitación de algunos géneros de la tribu Spermaceae (Rubiaceae) ha planteado dificultades que se manifiestan en el distinto criterio de los autores sobre este tema.

Schumann (1891) reconoció en esta tribu 18 géneros, 13 de los cuales estaban representados en América. Posteriormente a esta lista se sumaron nuevos géneros de 1 ó 2 especies: *Diacrodon* Sprague, *Diodella* (Torr. & A. Gray) Small, *Microsepalum* Urb., *Tortuella* Urb., *Spermaceodes* Kuntze, *Tobagoa* Urb., que no han sido totalmente aceptados. Sin embargo la mayoría de los autores en estudios florísticos regionales han seguido en término generales el criterio de Schumann, introduciendo sólo cambios menores. Verdcourt (1975: 301) señaló la dificultad en reconocer ciertos géneros casi únicamente por la dehiscencia de los frutos, sobre todo ante material florífero y además

por el escaso valor que él le asigna a este carácter unitario. Este autor amplía los límites de *Spermaceae* L. y subordina a éste las especies de *Borreria* G. Mey. y *Diodia* L., si bien resalta que *Diodia virginiana* L., especie americana y tipo del género, tiene frutos de estructura diferente a las especies de *Diodia* del área africana. Verdcourt (1975) señaló que Steyermark (en litt.) concordó en gran parte con su opinión, pero a pesar de ello reconoció a estos tres géneros separadamente, ya que admitió que se podían diferenciar bien, evitando de este modo numerosos cambios nomenclaturales. En el tratamiento de las Rubiáceas de Venezuela, Steyermark (1974) mantuvo este criterio. Actualmente algunos autores se inclinan por apoyar con variantes el criterio de Verdcourt, así Chaw y Sivarajan (1989), Fosberg et al. (1981), Howard (1989) y Bur-

¹ Esta comunicación constituye una parte del trabajo Delimitation of the American Genera of the Tribe Spermaceae (Rubiaceae) presentado durante la International Conference on the Systematics of the Rubiaceae (1993), St. Louis, Missouri. Se agradece a Angel Cabrera que realizó las diagnosis latinas y a los curadores de los herbarios de Brasil (MBM, PACA, R, RB, SP, SPF), Estados Unidos (F, MO, NY, US) y Argentina (BA, BAB, CTES, LP, SI) que nos facilitaron sus colecciones.

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Tabla 1. Caracteres del *Ebelia* subg. *Ebelia* y del subg. *Galianthe*.

Subg. <i>Galianthe</i>	Subg. <i>Ebelia</i>
Fruto de mericarpos dehiscentes	Fruto de mericarpos indehiscentes
Flores siempre heterostilas	Flores casi siempre heterostilas, excepto en <i>G. dichotoma</i>
Semillas a veces complanadas, con bordes aliformes	Semillas nunca complanadas
Hábito erecto, con frecuencia xilopodio muy desarrollado	Hábito variado, erecto, postrado, trepador
Tallo nunca alado	Tallo casi siempre alado
Cromosomas $x = 8$	Cromosomas $x = 14, 15$
Cerca de 40 sp., América del Sur	9 sp., Centro y Sudamérica
10°–35°S	20°N–35°S

ger y Taylor (1993) reconocieron *Diodia* y *Spermacoce* y subordinaron en este género las especies de *Borreria*.

De ahí que un estudio global de los géneros de Spermaceae analizando el mayor número de caracteres de las especies que los representan, es necesario para fundamentar los límites y las relaciones de los mismos. Con este fin se ha continuado con el estudio de los géneros *Diodia* y *Borreria*. De estos se han separado algunas pocas especies que por sus caracteres se han asimilado al género *Galianthe* (Cabral, 1991; Pire & Cabral, 1992), pero del que se diferencian por los frutos de mericarpos indehiscentes. Por esto se propone ampliar los límites del mismo e incluir las especies estudiadas en un nuevo subgénero: *Galianthe* subg. nov. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo.

MATERIALES Y MÉTODOS

Este estudio se ha realizado con material de los herbarios nacionales y extranjeros cuyas siglas se registran de acuerdo con Holmgren et al. (1990) (BA, BAB, BR, CTES, F, HAS, ICN, G, K, LIL, LP, MBM, MNES, MO, NY, P, PACA, R, RB, SI, SP, SPF, US).

TRATAMIENTO TAXONÓMICO

En el estudio emprendido de las especies americanas de los géneros *Spermacoce*, *Borreria* y *Diodia* se han separado unas especies que no reúnen los caracteres de estos géneros: *Borreria dichasia* Sucre & C. G. Costa; *Diodia brasiliensis* Spreng., *D. brasiliensis* var. *angulata* (Benth.) K. Schum., *D. cymosa* Cham., *D. dichotoma* (Willd. ex Roem. & Schult.) K. Schum. y *D. hispidula* A. Rich. ex DC.; y *Spermacoce bogotensis* Kunth.

De esta lista, *Diodia dichotoma* fue descrita erróneamente en el género *Knoxia* L., ya que este género es considerado actualmente en una tribu independiente, Knoxieae, que se caracteriza por presentar flores con óvulos de placentación apical,

péndulos, de micrópila súpera. Este error fue enmendado y la especie fue reubicada sucesivamente en los géneros *Spermacoce*, *Borreria*, y *Triodon* DC. por distintos autores y finalmente como *Diodia dichotoma* (Schumann, 1889).

Borreria dichasia fue descrita como *Borreria* a pesar de no haber contado con material con frutos. *Diodia cymosa* y *D. hispidula* fueron descritas dentro del género *Diodia* por sus frutos de mericarpos indehiscentes. *Spermacoce bogotensis* fue reubicada en el género *Diodia* o *Borreria* por distintos autores.

Diodia brasiliensis Spreng. fue separada por De Candolle (1830) junto con *D. anthospermoides* Cham. & Schltld. y *D. polymorpha* Cham. & Schltld., en un nuevo género, *Triodon*. Este autor caracterizó a dicho género por el hábito sufruticoso, las inflorescencias en fascículos espigados y los frutos de mericarpos indehiscentes y lo nominó haciendo alusión a los tres diminutos dientecitos, correspondientes a restos de hacecillos vasculares, persistentes en el ápice de los pedicelos al caer los frutos. Posteriormente Bentham agregó dos nuevas especies, *Triodon angulatum* de México y *T. laxum* de Ecuador. Este género no fue aceptado por algunos autores (Schumann, 1888; Standley, 1930; Steyermark, 1974) y posteriormente sus especies se reconocieron dentro del género *Diodia*, como uno, dos ó tres taxones distintos, por tener frutos de mericarpos indehiscentes. De Candolle al describir *Triodon* no registró el dimorfismo floral, a pesar de que incluyó como basónimo de *T. polymorphus* a *Diodia polymorpha* Cham. & Schltld. En esta especie sus autores diferencian variedades y dan una descripción detallada de las flores brevistilas y longistilas que tienen, si bien no usan estos términos. Schumann (1889) consideró a las tres especies citadas por De Candolle, sinónimos de *Diodia polymorpha*, a pesar de que registró a una especie anterior *D. brasiliensis* Spreng. (1825) entre sus sinónimos.

El grupo de especies aquí estudiado se corresponde con los caracteres del género *Triodon*, pero este nombre genérico está invalidado por un homónimo anterior (Tabla 1) y en su lugar debe usarse *Ebelia*

Rchb. Pero *Ebelia* es muy similar a *Galianthe* Griseb., género rehabilitado recientemente (Cabral, 1991; Pire & Cabral, 1992). Ambos presentan inflorescencias amplias de ramificación cimosa, flores dimorfas y difieren por los frutos, de mericarpos dehiscentes en *Galianthe* e indehiscentes en *Ebelia*. Por lo tanto se propone ampliar los términos de la definición de *Galianthe* y subordinar *Ebelia* como: *Galianthe* Griseb. subg. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo.

En este nuevo subgénero se incluyen los siete taxones mencionados y tres especies nuevas de la flora brasileña: *Galianthe humilis* E. L. Cabral & Bacigalupo, *Galianthe polygonoides* E. L. Cabral & Bacigalupo y *Galianthe vaginata* E. L. Cabral & Bacigalupo.

***Galianthe* Griseb.**, Abh. Königl. Ges. Wissensch. Göttingen 24: 157. 1879. *Borreria* G. Mey. sección *Galianthe* (Griseb.) K. Schum., en Martius, Fl. Brasil. 6(6): 40–42. 1888. *Borreria* G. Mey. subg. *Galianthe* (Griseb.) Standl., Field Mus. Hist. Bot. Ser. 8 (5): 392. 1981. TIPO: *Galianthe fastigiata* Griseb.

Se amplian los límites de *Galianthe* y se reconocen dos subgéneros sobre la base de la diferencia de dehiscencia de los frutos:

- 1a. Frutos de mericarpos dehiscentes ... subg. *Galianthe*
1b. Frutos de mericarpos indehiscentes ... subg. *Ebelia*

***Galianthe* Griseb. subg. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo**, comb. et stat. nov. *Ebelia* Rchb., Deut. Bot. Herb. Buch. 74. 1841. *Triodon* DC., Prodr. 4: 566. 1830, non Baumg. (1816). TIPO: *Triodon polymorphus* DC. [= *Galianthe brasiliensis* (Spreng.) E. L. Cabral & Bacigalupo] (lectótipo, aquí designado).

Hierbas perennes, sufrútices o pequeños arbustos, erectos, trepadores o postrados. Tallos tetragonos, en general alados. Hojas con la nervadura marcada o apenas visible. Vaina estipular fimbriada, breve, rara vez tubulosa, prolongada por encima de la inserción del par de hojas correspondiente. Inflorescencias complejas, tirsoideas o cimoidales, inflorescencias parciales en dicasios más o menos congestos, en fascículos o cabezuelas subglomeriformes, rara vez inflorescencias simples, en cimoides laxos. Flores tetrámeras, heterostilas, pilosas en el interior del tubo corolino. Frutos de dos mericarpos indehiscentes, con línea de dehiscencia preformada sobre la línea media de la cara adaxial. Semillas reticuladas o foveoladas con estrofiolo en la cara placentar. Granos de polen isopolares, radiosimétricos, entre 25–50 µm, oblato-esferoidales o prolato-esferoidales, estéfano-colporados, de exi-

na semitectada-reticulada, con retículo complejo o simple (*Galianthe bogotensis* y *G. dichotoma*) (Pire, 1996). $2n = 28$ (*G. bogotensis*); $n = 15$ (*G. brasiliensis* subsp. *angulata*). [Los otros detalles bajo *G. brasiliensis* subsp. *angulata*.]

CLAVE PARA DIFERENCIAR LAS ESPECIES DE *GALIANTHE* SUBG. *EBELIA*

- 1a. Vaina estipular tubulosa, prolongada por encima de la inserción del par de hojas correspondiente.
2a. Vaina pilosa; tallos de ángulos alados; Brasil 9. *G. vaginata*
2b. Vaina glabra; tallos sin alas; Brasil 8. *G. polygonoides*
- 1b. Vaina estipular breve, no sobrepasando la inserción del par de hojas correspondiente.
3a. Hojas sólo con el nervio medio visible.
4a. Inflorescencias simples, en cimoides laxo, nudos floríferos con flores solitarias; Ecuador, Perú 5. *G. dichotoma*
4b. Inflorescencias compuestas, nudos floríferos con flores en fascículos o glomérulos.
5a. Cáliz de 4 sépalos; inflorescencias compuestas cimoidales, inflorescencias parciales subglomeriformes; Colombia 1. *G. bogotensis*
5b. Cáliz de 2 ó 4 sépalos; inflorescencias compuestas, tirsoideas-espiciiformes o cimoidales, inflorescencias parciales en fascículos; México a Argentina 2. *G. brasiliensis*
- 3b. Hojas con nervios secundarios surcados en el haz y en resalto en el envés.
6a. Inflorescencia cimoidal con inflorescencias parciales congestas, subglomeriformes.
7a. Tallos de ángulos notoriamente alados; hojas 6–20 mm lat.; Brasil, Paraguay, Uruguay, Argentina 4. *G. dichasia*
7b. Tallos de ángulos oscuramente alados; hojas 1–7 mm lat.; Brasil 3. *G. cymosa*
- 6b. Inflorescencia cimoidal de ramas cincinoides, con inflorescencias parciales paucifloras, fasciculadas.
8a. Tallos simples; frutos sub-hemisféricos de 1.6–2 mm long.; Brasil, Paraguay, Argentina ... 6. *G. hispidula*
8b. Tallos ramificados; frutos turbina-dos de 5 mm long.; Brasil 7. *G. humilis*

1. *Galianthe bogotensis* (Kunth) E. L. Cabral & Bacigalupo, comb. nov. Basónimo: *Spermacoce bogotensis* Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Quarto ed. 3: 347, Folio ed. 3: 271. 1819. *Diodia bogotensis* (Kunth) Cham. & Schltl., Linnaea 3: 350. 1828. *Borreria bogotensis* (Kunth) Standl., Publ. Field Columbian Mus., Bot. Ser. 7: 160. 1930. TIPO: Colombia. Crescit juxta urbem Santa Fe de Bogotá, alt. 1370 hex, *Humboldt & Bonpland s.n.* (holótipo, B destruido; foto F860, CTES, SI; lectótipo, aquí designado, P). Figura 1.



Borreria anthospermoides DC., Prodr. 4: 550. 1830. TIPO: Colombia. In Amer. austr. prope Sta.-Fe de Bogotá, colector desconocido, ex herb. Delessert, 1816 (holótipo, G; foto F6689, CTES, SI).

Sufrútice muy ramificado, semipostrado a prostrado, formando una extensa mata, de tallos radican-tes, estrechamente alados, glabros, escabriúsculos o pilósulos hacia el ápice de los entrenudos, con brotes axilares que dan apariencia verticilada a los nudos foliares. Hojas de 6–18 × 1.5–4 mm, angostamente elípticas u ovals, de base y ápice agudos y margen revoluto, sólo con la vena central manifiesta, subglabras, escabriúsculas sobre el margen, a veces algo sobre el haz y la vena media en el envés. Vaina estipular de 1–2.5 mm long., pubescente, con 5–7 lacinias de 2.5–4 mm long. Inflorescencia terminal cimoidal, con inflorescencias parciales, subglomeriformes, a veces en ramas laterales reducidas a 1 sola cabezuela. Cáliz con 4 segmentos triangulares y algún dientecito intercalar, sólo en los bordes escabriúsculos. Hipanto turbinado de 1.5–2.5 mm long., glabro a subglabro. Corola blanca, micropapilada en la superficie externa; disco entero. Flor brevistila: corola de 3.5–5 mm long., con lóbulos iguales o más cortos que el tubo corolino en su interior con pelos moniliformes cortos y delgados sobre el tubo y pelos gruesos sobre el tercio inferior de los lóbulos; anteras de 1–1.5 mm long. y filamentos estaminales de 0.6–1.2 mm long.; estilo de 1.5–3 mm long., de ramas estilares filiformes de 0.5–1.8 mm long. Flor longistila: corola de 4–5.5 mm long., de lóbulos más cortos que el tubo, de superficie interna con pelos dispersos sobre el tubo y pelos más densos, gruesos y largos en la base de los lóbulos; anteras de 1–1.3 mm long. y filamentos de 0.5–1 mm; estilo de 4–5 mm y ramas estilares de 2.5–0.9 mm long. Fruto de 2–3.2 mm long., glabro, de mericarpos indehiscentes. Semilla de 2–2.3 mm long., superficie foveolada, con ancho surco longitudinal en la línea media ventral, cubierto parcialmente por el estrofiolo.

Distribución (Fig. 11). Habita en el páramo o en área vecina en Colombia, entre 2200–3575 m s.m., en borde de ciénagas, matorral subserial, pastizal o rastrojos.

Material examinado. COLOMBIA. Nueva Granada, 1857, *Triana* 75 (NY, P). **Boyacá:** Cordillera Oriental, Páramo de Belén, 6 mayo 1959, *Barclay & P. Juajibioy*

7573 y 7661 (MO, NY); Socha, 8 nov. 1944, *Fosberg* 22225 (NY); Santuario de Yguaque, 26 mar. 1981, *Melampy* 1313 (MO). **Cundinamarca:** Boquerón de Chiquaque, 16 mar. 1939, *Killip* 34201 (F, NY); Páramo de Guasca, 15 dic. 1938, *Balls* 5696 (K); Páramo de Siberia, 25 oct. 1952, *Humbert et al.* 26929 (SI); Macizo de Bogotá, 7 mayo 1946, *Schultes* 7259 (F); Macizo de Bogotá, Quebrada de Chicó, 25 mayo 1939, *Cuatrecasas* 5007 (F), dic. 1946, *Black* 46-441 (F); Cordillera Oriental, Páramo, 16 nov. 1959, *García Barriga* 16136 (NY); above Bogotá, 16 ago. 1917, *Rusby et al.* 1260 (NY); 12 km WSW of Junín, on the Río Blanco, small affluent of the río Piedras, 19 Feb. 1944, *Fosberg* 21484 (NY); Río San Francisco, above Bogotá, 13 set. 1917, *Pennell* 1934 (NY); Sabana of Bogotá, supra hill, 4 Feb. 1945, *Schiefer* 402 (F); Bogotá, Nov. 1852, *Holton* 417 (K), 29 Oct. 1975, *André* 728 (K); above La Cita, 10 mayo 1946, *Schultes* 7122 (F); près de Bogotá, *Triana* 3123 (P); Boquerón de Bogotá, 21 nov. 1975, *André* 72 (K); Bogotá, 20 set. 1913, *Apolinar* 74 (F); Montecillo E of Guatavita, 29 mayo 1947, *Haught* 5774 (F); Paipa, ene. 1938, *Jimenez* 68 (F).

Esta especie se parece por sus inflorescencias a *G. cymosa* y *G. dichasia*, pero se diferencia de ambas por sus hojas más pequeñas y subnervias. Su área está restringida a los páramos de Bogotá y zonas circunvecinas, mientras que las otras dos especies son del SE del Brasil, la primera citada sólo para el estado de Paraná y la segunda desde Paraná llega hasta el Paraguay, Argentina y Uruguay; ambas de terrenos bajos y húmedos.

2. *Galianthe brasiliensis* (Spreng.) E. L. Cabral & Bacigalupo, comb. nov. Basónimo: *Diodia brasiliensis* Spreng., Syst. Veg. 1: 406. 1824. TIPO: Brasil, Sello (holótipo, B destruido); Brasil. Sin loc., año 1828, *Pohl* s.n. (neótipo, aquí designado, G; foto F6728, SI).

Subarbusto de 0.30–0.70(–1) m de alto. Tallos tetraedros, de ángulos marginados a estrechamente alados, glabros a hírtulos. Hojas opuestas, o en general seudoverticiladas, 3–35 × 0.7–11 mm, ovadas o elípticas, agudas, atenuadas en seudopécíolo, escabriúsculas en el margen y los nervios en el envés a glabras, nervadura poco visible, con excepción del nervio medio; vaina estipular 3–7 laciniada, glabra o hispídula. Inflorescencia frondosa a bracteada, tirsoide, espiciforme a pleiotirsoide con inflorescencias parciales también espiciformes o cimoidal, de ramificación dicásial a monocásial, siempre con flores congestas, fasciculadas en los nudos floríferos. Flores brevemente pediceladas. Cáliz 2 ó 4 partido, con dientecitos intercalares. Hipanto turbinado, glabro o hírtulo. Corola

4-lobada, 2–3.5 mm long., algo pilosa en su interior. Flor brevistila: anteras 1–1.25 mm, filamentos estaminales 1 mm y estilo 1.3–1.5 mm long. Flor longistila: anteras 0.5–1 mm, filamentos estaminales muy breves y estilo 2.5–3.5 mm long. Fruto 1.5–2.5 mm long., turbinado, algo comprimido lateralmente, hispídulo. Semilla 1–2 mm long., finamente reticulada, reniforme en corte transversal, con leve y amplia depresión longitudinal cubierta por el estrofolo.

Esta especie cubre dos áreas de dispersión, una amplia en Sudamérica, desde Bahía a Rio Grande do Sul en Brasil, Paraguay, Uruguay y NE de la Argentina hasta la ribera bonaerense del Río de La Plata. La otra área está restringida al S de México, Belice y Guatemala. En relación con la distribución se puede señalar que el material de México y áreas vecinas es uniforme en sus caracteres, no así el sudamericano que presenta variaciones principalmente en el tamaño de las hojas, a veces en un mismo ejemplar, en el desarrollo de las inflorescencias y en el número de los segmentos del cáliz. Las mismas han sido registradas por los autores en distintas variedades, las cuales resultan difíciles de reconocer en su mayoría por las transiciones observadas en los ejemplares estudiados. Hasta donde se ha podido estudiar los ejemplares con cáliz 2 ó 4-mero se corresponden con inflorescencias algo diferentes. Las muestras con cáliz de 2 segmentos mayores presentan inflorescencias tirsoide-espícoformes o pleiotirsoideas con paracladios también espícoformes. Las muestras con cáliz 4-partido, de segmentos similares, presentan inflorescencias tirsoideas pero en parte con ramificación cimoidal, con paracladios que superan el eje principal. En ambos casos los nudos floríferos tienen flores fasciculadas. De ahí que en el presente trabajo y hasta tanto no se realice una revisión más completa, principalmente de los herbarios brasileños, se propone aceptar a todo el material sudamericano como *G. brasiliensis* subsp. *brasiliensis*, y con respecto al material de México, Belice y Guatemala, aceptarlo como *G. brasiliensis* subsp. *angulata* (Benth.) E. L. Cabral & Bacigalupo, por sus caracteres uniformes y área restringida.

CLAVE PARA DIFERENCIAR LAS SUBESPECIES DE *GALIANTHE*
BRASILIENSIS

- 1a. Cáliz 2 ó 4-partido; inflorescencias tirsoide-espícoformes o de ramificación parcialmente cimoidal, con el eje principal más corto que los laterales; Sudamérica subsp. *brasiliensis*
1b. Cáliz 4-partido; inflorescencias notoriamente tirsoide-espícoformes; México, Centroamérica
..... subsp. *angulata*

2a. *Galianthe brasiliensis* subsp. *brasiliensis*
(Fig. 2)

Diodia anthospermoides Cham. & Schltdl., Linnaea 3: 343. 1828. *Triodon anthospermoides* (Cham. & Schltdl.) DC., Prodr. 4: 566. 1830. *Diodia polymorpha* var. *anthospermoides* (Cham. & Schltdl.) K. Schum., in Mart., Fl. Bras. 6(6): 12. 1888. TIPO: Brasil. In Brasilia aequinoctiali, Sellow (holótipo, B destruido); Brasil. Rio de Janeiro: 1883–84, Glaziou 14926 (neótipo, aquí designado, K).

Diodia polymorpha Cham. & Schltdl., Linnaea 3: 344. 1828. TIPO: Brasil. E Brasilia tropica extratropica magnam speciminum varieta tumque copiam misit Sellow (holótipo, B destruido); Brasil. Paraná: Mato Preto, G. Hatschbach 33869 (neótipo, aquí designado, MBM; isoneótipo, SI).

Diodia polymorpha var. *macrophylla* Cham. & Schltdl., Linnaea 3: 345. 1828. TIPO: Brasil. E Brasilia meridionali, Sellow (holótipo, B destruido); Argentina. Entre Ríos: Concepción del Uruguay, Lorentz 1799 (neótipo, aquí designado, CORD).

Diodia polymorpha var. *microphylla* Cham. & Schltdl., Linnaea 3: 345. 1828. *Triodon polymorphus* var. *microphyllus* (Cham. & Schltdl.) DC., Prodr. 4: 566. 1830. *Diodia polymorpha* var. *microphylla* (Cham. & Schltdl.) Standl., Publ. Field Columbian Mus., Bot. Ser. 8: 387. 1931. TIPO: Brasil. E provincia Rio Janeiro proveniens, Sellow (holótipo, B destruido; lectótipo, aquí designado, K material estéril).

Triodon glomeratus DC., Prodr. 4: 566. 1830. TIPO: Brasil. In Brasilia, Pohl s.n. (holótipo, G; foto F6728, SI).

Sufrútice con hojas de 3–35 mm long. × 0.7–11 mm lat., elípticas, a veces algunas obovadas. Inflorescencias tirsoide-espícoformes o pleiotirsoideas con paracladios espícoformes, nudos floríferos con flores fasciculadas. Cáliz de 4 segmentos subiguales o 2 segmentos mayores y dientecitos intercalares mucho menores.

Distribución (Fig. 11). Brasil, Paraguay, Uruguay y NE de la Argentina hasta el delta del río Paraná y costa ribereña de Buenos Aires.

Material seleccionado. BRASIL. **Bahía:** Munic. do Livramento do Brumado, Río Contas, 19–20 jul. 1979, Mori et al. 12310 (K); Río do Contas, Salto do Fraga, 6 abr. 1992, Hatschbach 56688 (CTES). **Minas Gerais:** sin fecha, Widgren 199 (K); Poços de Caldas, Veu das Noivas, 19 ene. 1980, Krapovickas et al. 35396 (CTES); São Thome das Letras, Serra do Cantagalo, 3 nov. 1984, J. Pirani et al. s.n. (CTES, K, SPF). **Paraná:** Serra do Mar, Porto do Cima, 2 ene. 1914, Dusén 14297 (K); Mun. Iguazú, 20 ene. 1949, Schwarz 7239 (CTES); Ríos dos Patos, 27 mar. 1947, Hatschbach 668 (CTES); Fernandes Penheiro, 27 mar. 1904, Dusén 4331 (SI). **Rio de Janeiro:** abr. 1875, Glaziou 7671 (K), abr. 1975, Glaziou 7670 (K), Serra do Itataia, sin fecha, Pereira 7088 (LP). **Rio Grande do Sul:** Pareí prope Montenegro, 31 mar. 1950, Rambo 46526 (K); Alegrete, Río Ibirá Puitan, 13 mar. 1948, Palacios-Cuezzo 1829 (CTES); São Sepe, 22 feb. 1948, Palacios-Cuezzo 1555 (CTES); Cachoeira do Sul, 19 feb. 1948, Palacios-Cuezzo 1068 (CTES); Arroio dos Ratos, dic. 1973, Mariath 150 (CTES); Morro do Coco, 20 jun. 1973, Lindeman et al. s.n. (CTES, ICN), 21 abr. 1974, Porto 595 (CTES). **Santa Catarina:** Munic. Ybirama, Smith et al. 7599 (K). **São Paulo:** Munic. São Paulo, Inst. de Botânica, 17 ene. 1968, Eiten 8090 E (K); Inter Muggy et São

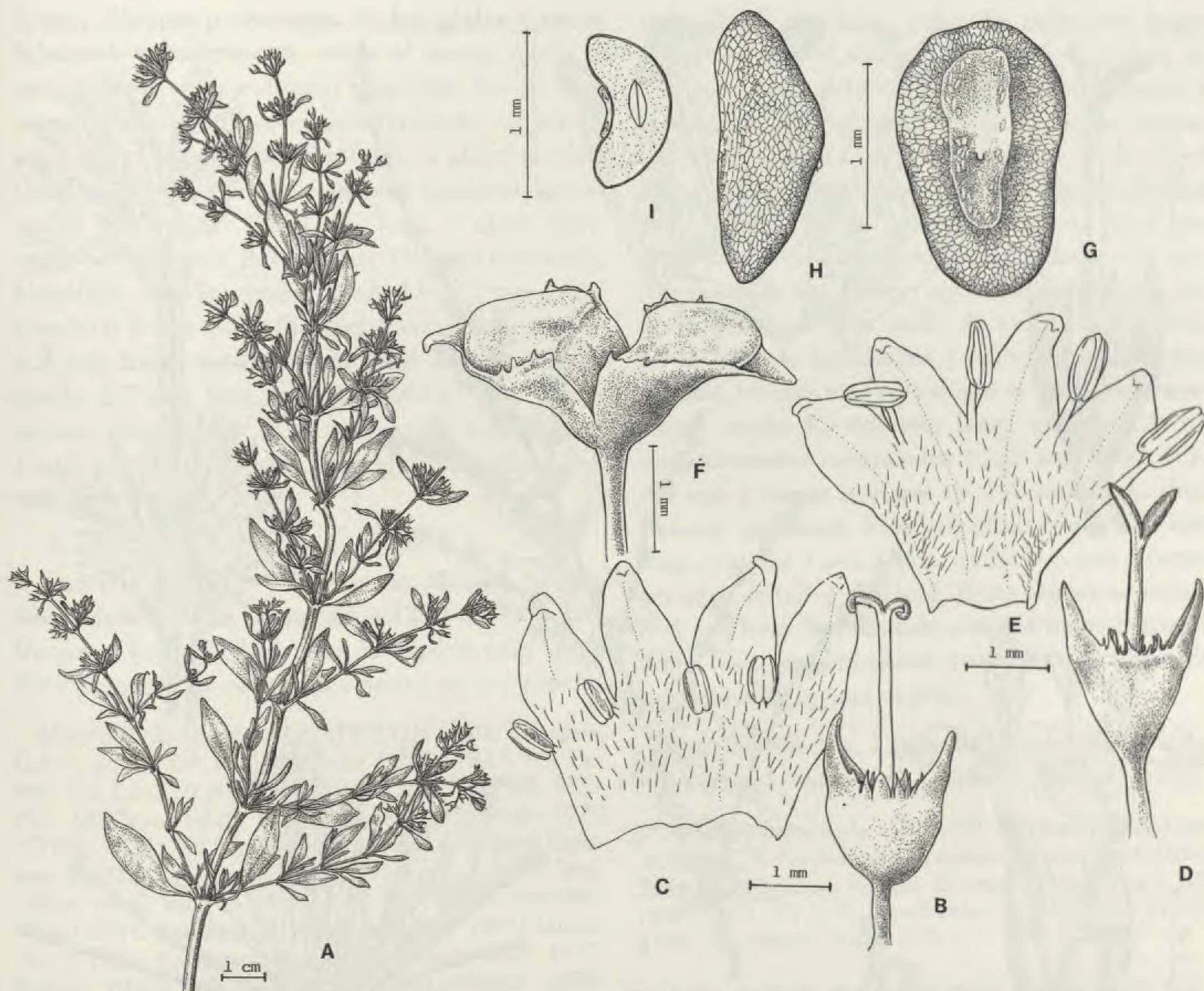


Figura 2. *Galianthe brasiliensis* subsp. *brasiliensis*. —A. Rama. —B, C. Flor longistila. —D, E. Flor brevistila. —F. Fruto. —G–I. Semilla, cara ventral, perfil y corte transversal. A, Burkart 4492; B, C, Burkart 20002; D, E, Burkart 18202; F–I, Burkart 3844.

Paulo, nov. 1833, *Riedel 1518* (K); Mun. de Campos do Jordão, 20 mar. 1969, *Souza s.n.* (CTES). PARAGUAY. In regione lacus Ipacaray, Nov. 1913, *Hassler 12709* (G). **Alto Paraná:** Puerto Gibajas, 28 mar. 1970, *Krapovickas et al. 15765* (CTES); Irala, 23 nov. 1950, *Montes 9866* (CTES); Pto. Indio, 6 set. 1981, *Caballero Marmorini 889* (CTES). **Itapúa:** Encarnación, 18 ene. 1944, *Rojas 10889* (CTES), 19 nov. 1945, *Bertoni 2401* (CTES); Isla Yaciretá, 3 feb. 1982, *Bordas 3039* (CTES). URUGUAY. Fray Bentos, 14 feb. 1877, *Fruchard s.n.* (P). ARGENTINA. **Misiones:** Apóstoles, San José, Escuela Agrotécnica P. Gentilini, potrero San Lorenzo, 12 feb. 1973, *Cabrera & Sáenz 29137* (SI); Cainguás, Puerto Rico, 4 mar. 1948, *Schwindt 629* (CTES); Candelaria, Ruinas Jesuíticas de Sta. Ana, 29 jun. 1986, *Ferrucci et al. 436* (CTES); Capital, Posadas, costa del río, 24 nov. 1949, *Bertoni 4796* (CTES); Guaraní, Ayo. Paraiso y Ruta 2, 23 set. 1993, *Rodríguez et al. 763* (CTES, MNES); Iguazú, Parque Nacional Iguazú, 7 ago. 1991, *Vanni et al. 2751* (CTES); San Ignacio, Teyucuaré, 4 abr. 1946, *Montes 2100* (CTES); San Pedro, Ayo. Liso, 22 set. 1945, *Bertoni 2076* (CTES). **Corrientes:** Berón de Astrada, Tuyuty, 3 mayo 1945, *Huidobro 2137* (CTES); General Paz, 12 km E de Itá Ibaté, costa del río Paraná, *Mroginski et al. 680* (CTES); Itatí, 18 abr. 1971, *Mroginski 149* (CTES); Santo Tomé, Ea. Timbó, 2 mar. 1983, *Schinini et al. 23794* (CTES); Ituzaingó, Em-

palme Ruta 34 y Ruta 14, 22 feb. 1980, *Cabral 160* (CTES); San Cosme, Paso de la Patria, 17 jun. 1945, *Worth 130* (CTES). **Entre Ríos:** Concordia, Salto Grande, 20 dic. 1961, *Burkart 23139* (SI); Gualeguaychú, Delta, arroyo Brazo Largo, mar. 1937, *Burkart 8298* (CTES, SI); Gualeguaychú, Landa, *Soriano 393* (BAB). **Buenos Aires:** Delta del Paraná, Paraná de las Palmas y Canal 6, 20 oct. 1938, *Mollura 17* (SI); Isla Martín García, 2 mayo 1948, *Soriano s.n.* (SI 22704).

2b. *Galianthe brasiliensis* subsp. *angulata* (Benth.) E. L. Cabral & Bacigalupo, stat. nov. Basónimo: *Triodon angulatum* Benth., Pl. Hartw.: 70. 1840. *Diodia polymorpha* var. *angulata* (Benth.) K. Schum., in Mart., Fl. Bras. 6(6): 13. 1888. *Diodia brasiliensis* var. *angulata* (Benth.) Standl., Carnegie Inst. Wash. Publ. 461: 90. 1935. TIPO: México. Textolcingo in montibus Chinantla, *Hartweg 507* (holótipo, K no visto). Figura 3.

Arbusto de tallos algo hispídulos, ángulos estrechamente alados, glabros. Hojas 5–18 mm × 1.5–

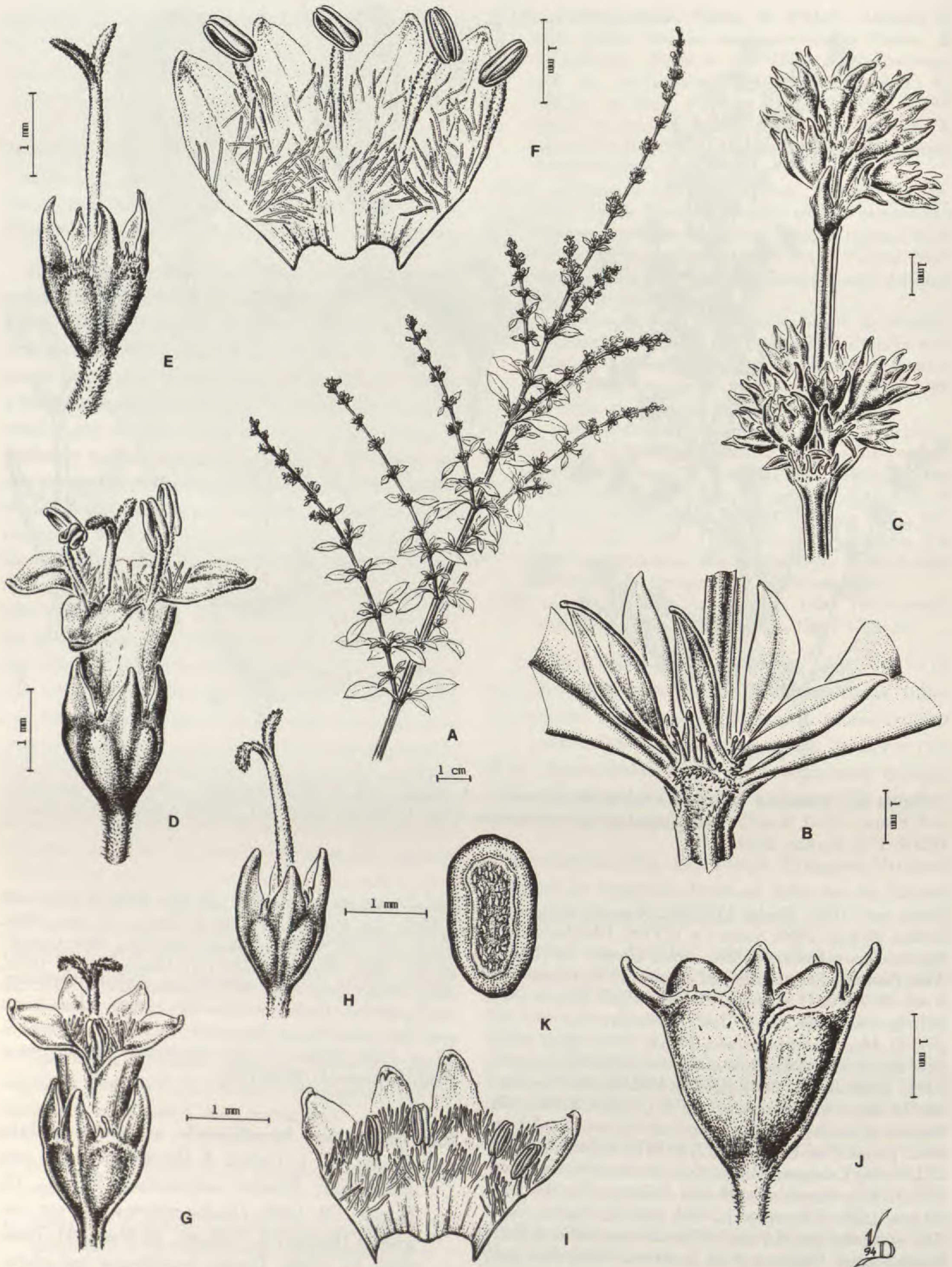


Figura 3. *Galianthe brasiliensis* subsp. *angulata*. —A. Rama. —B. Vaina estipular. —C. Detalle de la inflorescencia. —D–F. Flor brevistila. G–I. Flor longistila. —J. Fruto. —K. Semilla. A, Schnee & Maury s.n.; B–F, Avendano et al. 00446; G–I, Breedlove 52678; J, K, Turckheim II-1605.

6 mm, elípticas u obovadas, de haz glabro y envés raramente escabriúsculo sobre el nervio medio y secundarios; vaina estipular hispídula, con 5–7 lacinas glabras. Inflorescencias tirsoideas espiciformes, con 4 a 14 nudos floríferos, o pleiotirsoideas. Cáliz 4-partido, con 2 segmentos opuestos ligeramente mayores, de 0.8–1 mm long., y algún diente en los senos intercalares. Hipanto turbinado, hispídulo. Flor longistila: corola 1.9–2.2 mm long., anteras 0.4–0.5 mm y filamentos estaminales 0.17–0.2 mm long., estilo 2 mm long. Flor brevistila: corola 2.7 mm long., anteras 0.6–0.7 mm y filamentos estaminales 1.15 mm; estilo 3–3.15 mm. Fruto 1.5(–2.5) mm long., hispídulo. Semilla 1.8–2 mm long.

Nombre vulgar. Tomillo silvestre.

Distribución (Fig. 11). Sur de México, Guatemala, Belice. Se la encuentra a 1350–1700 m s.m. Burger y Taylor (1993) citan la especie para Costa Rica pero dudan de que sea nativa en ese país.

Material examinado. GUATEMALA. **Alta Verapaz:** Cobán, ene. 1907, *von Türckheim 111605* (BAF, SI). **Petén:** San Luis, 10 jul. 1959, *Lundell 16271* (CTES). BELICE. **El Cayo:** Sibun River, 23 jun. 1955, *Gentle 8773* (CTES). MEXICO. Sin localidad, *Linden 615* (BR). **Chiapas:** Rayón, in the Selva Negra, 10 km above Rayón Mezcalapa along road to Jitotol, 10 Sep. 1981, *Breedlove 52678* (NY). **Hidalgo:** El Candeje, 4 jun. 1973, *Gimate 852* (CTES). **Veracruz:** Munic. de Totutla, 7 jul. 1977, *Ventura 14223* (G); Jicó, 5 jul. 1908, *Pringle 10803* (CTES); Tenejapa, 2 ago. 1979, *Avendano et al. 00446* (NY); environs d'Orizaba, *Botteri & Sumichrast 186* (P); Valle de Córdoba, 10 dic. 1865–66, *Bourgeau 1716* (BR, P); Córdoba, 4 ago. 1882, *Kerber 23* (BR). Sin dato de localidad ni fecha de colección, *Schnee & Maury s.n.* (P, SI).

Lewis (en Kiehn, 1986) registró, bajo el nombre de *Triodon angulatum*, como número cromosómico para esta especie $n = 15$ sobre un ejemplar de Veracruz, México.

3. *Galianthe cymosa* (Cham.) E. L. Cabral & Bacigalupo, comb. nov. Basónimo: *Diodia cymosa* Cham., *Linnaea* 9: 217. 1834. TIPO: Brasil. E *Brasilia tropica* misit Sellow (holótipo, B destruido; foto F 861 CTES, SI); Brasil. Paraná: Pinhais, 20 mar. 1952, *Tesmann et al. 749* (neótipo, aquí designado, MBM). Figura 4.

Sufrútice apoyante de 50–65 cm alt., con tallos gráciles, tetrágonos pubérulos a glabros, con alas muy estrechas, retrorso-escabriúsculas sobre los márgenes. Hojas angostamente elípticas, 10–35 × 1–7 mm, ápice acuminado y base atenuada, con 3 pares de nervios secundarios, subopuestos, escabriúsculas en la haz y sólo sobre los nervios en el envés margen revoluto, escabriúsculo. Vaina esti-

pular 2–2.5 mm long., pubérula, pelos más largos y densos hacia el margen, lacinas 5–6, glabras de 1–5 mm long. Inflorescencia cimoidal, dicasial a monocasial, con inflorescencias parciales densas, subglomeriformes. Cáliz 4 segmentos, 2 de 2.5–3 mm y 2 menores de 1.5–2 mm, con algunos dientes intercalares. Hipanto glabro, obcónico, 1.6–2 mm long. Corola externamente micropapilada, con papilas notables en el dorso apical de los lóbulos, superficie interna, con anillo de pelos moniliformes en la base de los lóbulos y pelos dispersos sobre el tubo, lóbulos más cortos que el tubo. Flor brevistila: corola 4.5–6.2 mm long., anteras 1.2–1.5 mm, filamentos estaminales 1.2–2 mm, estilo 2.5–3.5 mm y ramas estilares de 1–2 mm long., densamente papilosas. Flor longistila: corola 5–6 mm long., anteras 1.3–1.5 mm, estilo 5–6 mm y ramas estilares de 0.8–1 mm long. Fruto obcónico, glabro, 3–4 mm long. Semilla más o menos plano-convexa, 2 mm long., escrobiculada, con estrofolo cubriendo parcialmente la cara ventral.

Distribución (Fig. 11). Hasta el momento se la ha coleccionado solo en el Estado de Paraná, Brasil.

Material examinado. BRASIL. **Paraná:** 1833, *Gaudichaud 518* (G); Serrinha, in campo, 14 ene. 1904, *Dusén 2695* (G); Curitiba, Barigui, 28 ene. 1975, *Ferreira 186* (MBM, MO, NY, US); Mandirituba, río Mauricio, 23 feb. 1978, *Hatschbach 41460* (US).

Esta especie guarda estrecha relación con *Galianthe dichasia* por su porte y sus inflorescencias, pero ésta presenta tallos con alas desarrolladas y hojas más anchas.

4. *Galianthe dichasia* (Sucre & C. G. Costa) E. L. Cabral, Bol. Soc. Argent. Bot. 27: 242. 1991. Basónimo: *Borreria dichasia* Sucre & C. G. Costa, *Loefgrenia* 48: 2. 1970. TIPO: Brasil. Estado do Paraná: Curitiba, Aeroporto Afonso Penna, *Pereira 5158* (holótipo, RB; isótipo, HB). Figura 5.

Diodia cymosa Cham. var. *aculeolata* Hassl., *Feddes Rept. Spec. Nov.* 14: 168. 1915. TIPO: Paraguay. Guairá: Cordillera de Villa Rica, 1-1905, *Hassler 8650* (lectótipo, aquí designado, G; isoelectotipo, NY).

Hierba sufruticosa de 50–80 cm de alt., erecta, de tallos radicales los nudos basales, tetrágonos, fistulosos, ± hirsutos o glabros con ángulos muy marcados hasta alados, alas de 1.7 mm de ancho, retrorso-laciniadas en el margen. Hojas elípticas, 15–60 × 6–20 mm, de ápice agudo o acuminado y base atenuada, pilosas, escabriúsculas a subglabras en ambas caras, margen revoluto, con 3–5 pares de nervios subopuestos, impresos en el haz y



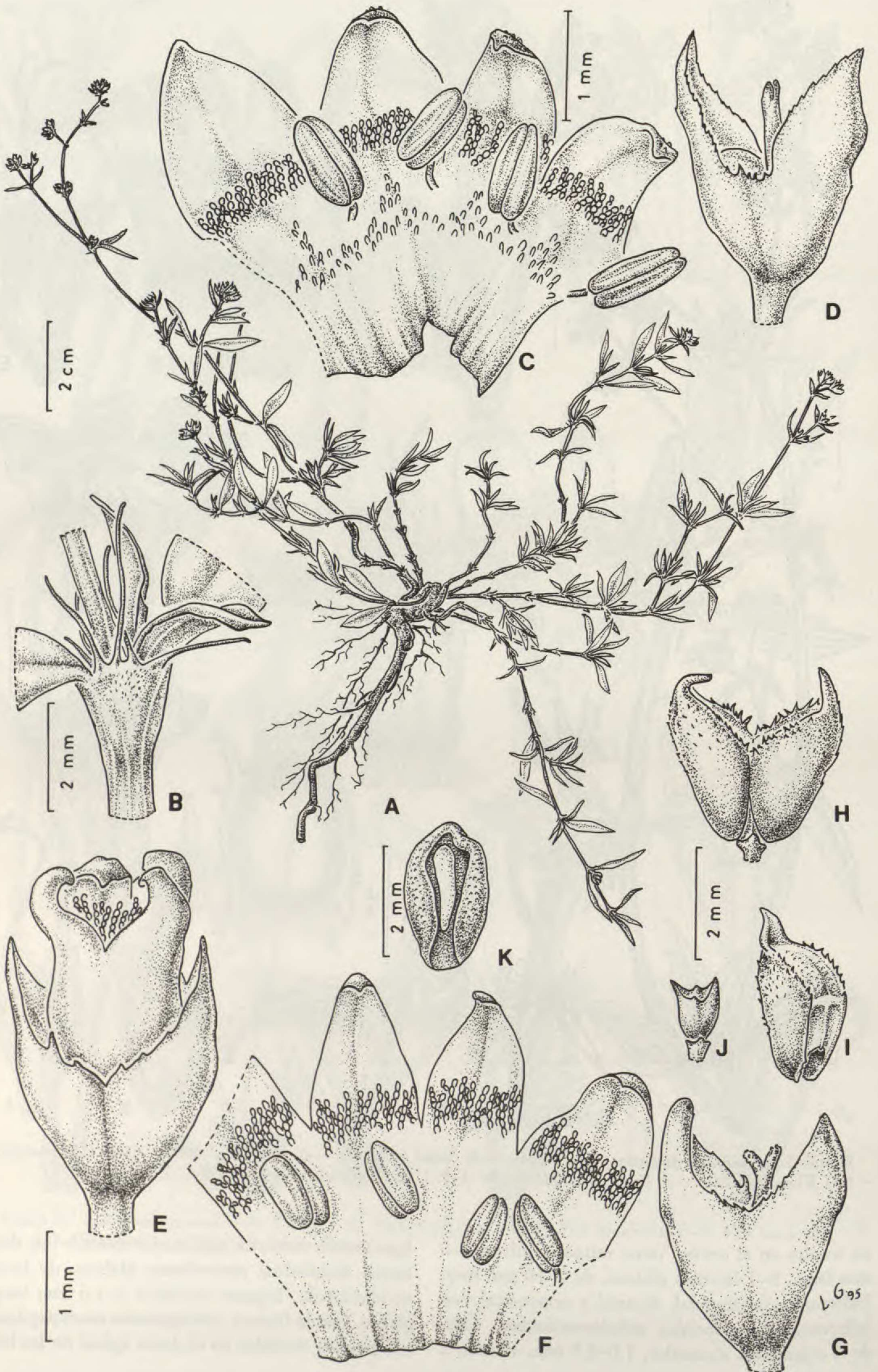
Figura 4. *Galianthe cymosa*. —A. Planta. —B. Vaina estipular. —C–E. Flor brevistila. F–H. Flor longistila. —I. Fruto. A–E, *Tesmann et al.* 749; F–I, *Dusén* 2695.



Figura 5. *Galianthe dichasia*. —A. Planta. —B. Vaina estipular. —C. Corte del tallo. —D–F. Flor brevistila. —G–I. Flora longistila. —J. Fruto. —K. Mericarpo. A–F, J, K, Krapovickas et al. 44888; G–I, Imaguire 2781.

en resalto en el envés. Vaina estipular pilosa, 3–5 mm long., 5–7 lacinias glabras, de 2–10 mm long. Inflorescencia cimoidal, dicasial a monocasial, con inflorescencias parciales subglomeriformes. Cáliz de 4 segmentos aleznados, 1.6–2.8 mm, a veces 2

ligeramente menores, opuestos, a menudo con diminutos dientecitos intercalares, glabros, de borde escabriúsculo, hipanto obcónico 1–1.5 mm long., glabro. Corola blanca, externamente micropapilada, con papilas notables en el dorso apical de los ló-



ulos, estos más cortos que el tubo, superficie interna con dos anillos de pelos moniliformes, uno sobre el tubo y otro de pelos algo más gruesos sobre la base de los lóbulos; disco entero. Flor brevistila: corola 4–5.2 mm, anteras 1–1.2 mm, filamentos estaminales 0.5–1.5 mm, estilo 2.5–4.7 mm, ramas estigmáticas de 2–2.2 mm de largo, con papilas densas. Flor longistila: corola 3.7–5 mm, anteras 0.7–1 mm, filamentos estaminales 0.2 mm y estilo de 4–5.8 mm long. Fruto 2.5–3.5 mm long. Semilla 2 mm de largo, plano-convexa con estrofiolo cubriendo parcialmente la cara ventral.

Distribución (Fig. 11). Esta especie vive en terrenos bajos, pantanosos, orilla de vertientes. Su área abarca el SE del Brasil (Paraná, Sta. Catarina y Rio Grande do Sul), Paraguay (San Pedro, Guairá), Uruguay (Rivera) y Argentina (Misiones).

Material examinado. BRASIL. **Paraná:** Rincao, 9 feb. 1947, *Hatschbach 624* (CTES, SP); Curitiba, 28 mar. 1950, *Tessmann 67* (MBM); 5 km E de Curitiba, 2 feb. 1973, *Krapovickas et al. 23093* (CTES, LP), 14 feb. 1978, *Krapovickas et al. 33657* (CTES); Piraquara, 3 mar. 1971, *Imaguire 2781* (ICN), 31 ene. 1967, *Dombrowski 2391* (CTES). **Santa Catarina:** Caçador, 22 dic. 1956, *Smith et al. 9073* (R). **Rio Grande do Sul:** Torres, Lagoa dos Quadros, 21 feb. 1950, *Rambo 45992* (CTES, LIL); Farroupilha, 7 feb. 1950, *Rambo 45708* (CTES); Caxias do Sul, 8 feb. 1955, *Rambo 56689* (PACA), 1 ene. 1949, *B. Rambo 30882* (PACA), 1932, *Augusto s.n.* (PACA); S. Leopoldo, 1907, *Theissen s.n.* (PACA); Bom Jesús, 13 ene. 1941, *B. Rambo 8521* (PACA), 15 ene. 1942, *Rambo 8839* (PACA); Ijuisinho, 30 ene. 1942, *Rambo 9961* (PACA); Cambará, feb. 1948, *Rambo 36712* (PACA). PARAGUAY. **San Pedro:** 10 km W de San Estanislao, bañado del río Tapiracuí, 19 feb. 1994, *Krapovickas et al. 44888* (CTES). URUGUAY. **Rivera:** Cunapirú, p. Rivera, 13 ene. 1941, *Rambo 3973* (PACA). ARGENTINA. **Misiones:** Gral. Belgrano, Ao. Pepirí Guazú, ene. 1983, *Guaglianone et al. 1147* (CTES, SI); Ldor. Gral. San Martín, Ao. Garuhapé, *Mroginski et al. 378* (CTES).

Galianthe dichasia guarda estrecha relación con *G. cymosa* de la que se diferencia por sus tallos más robustos, de ángulos bien marcados a manifiestamente alados y sus hojas anchas.

5. *Galianthe dichotoma* (Willd. ex Roem. & Schult.) E. L. Cabral & Bacigalupo, comb. nov. Basónimo: *Knoxia dichotoma* Willd. ex Roem. & Schult., Syst. Veg. 3: 532. 1818. TIPO: América meridionalis. Humboldt (holótipo, B no visto, foto B-W 2676, F 862, CTES, SI). Figura 6.

Diodia glabra Willd. ex Roem. & Schult., Syst. Veg. 3: 532. 1818, non Pers. (1805).

Spermacoce dichotoma Willd. ex Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Quarto ed. 3: 348; Folio ed. 3: 272. 1819. *Borreria dichotoma* (Willd. ex Kunth) Cham. & Schltdl., Linnaea 3: 340. 1828. *Diodia dichotoma* (Willd. ex Kunth) K. Schum., in Mart., Fl. brasil. 6 (6): 11. 1888. TIPO: Perú. Prope Peruvianorum et in declivitate montis ignivomi Tunguraguae, alt. 1400–1600 hex, Bonpland (holótipo, P, foto F37152, CTES, SI).

Triodon laxum [*Triodia laxa*] Benthham, Pl. Hartw.: 194. 1840. TIPO: Juxta ponte Guapulo, prope Quito, *Hartweg 1068* (holótipo, K no visto).

Sufrútice con ramas postradas de 10–30 cm long., tallos tetragonos con alas estrechas, de margen escabriúsculo. Hojas ovales, de 7–20 × 2–7 mm, ápice acuminado y base atenuada en corto pseudopecíolo, margen revoluto, escabriúsculo, discoloras, haz escabriúscula a glabra, con vena media surcada, poco conspicua, envés escabriúsculo sobre la vena media sobresaliente, y a veces sobre los 2–3 pares de nervios poco conspicuos. Vaina estipular 1.7–3.5 mm long., pilosa, con 3–7 lacinias glabras, de 1.5–4 mm long. Inflorescencia cimoides, dicasial, con brácteas foliáceas en los nudos basales, disminuyendo a linear-subuladas, diminutas en nudos apicales. Cáliz bipartido, de 2 segmentos triangulares, carnosos, de bordes escabriúsculos, casi siempre alternando con algunos dientecitos intercalares; hipanto obcónico, 1–1.2 mm long., escabriúsculo en la mitad superior. Corola 4(–5)-lobada, 2.5–3.8 mm long. de lóbulos más cortos que el tubo, micropapilada por fuera, con papilas notables en el dorso apical de los lóbulos y con pelos moniliformes en su interior. Anteras 0.7–0.8 mm long. y filamentos breves. Estilo 0.5–1.2 mm long., con ramas de 0.5 mm long. Fruto turbinado 3–3.5 mm long., escabriúsculo a subglabro. Semilla 2.5–3 mm long., subobovoide, de superficie foveolada, con estrecho surco en la cara ventral cubierto parcialmente por el estrofiolo.

Distribución (Fig. 11). Habita en zonas altas, entre los 2300–3340 m s.m. en Ecuador hasta el norte de Perú.

Material examinado. ECUADOR. **El Oro:** Hacienda Chepel, headwaters of Río San Luis, 22 km E of Zaruma, 13 Feb. 1945, *Fosberg & Giler 23007* (NY). **Loja:** upper Malacatos Valley, 15–20 km S Loja, 6 July 1944, *Prieto 36* (NY); Paso de Cajanuma above Pueblo Nuevo, 9 feb. 1945, *Fosberg & Giler 22889* (P); Loja, W of town, 3 Oct.

1955, *Asplund 17894* (G, P); San Pedro Loja, 26 abr. 1946, *Espinosa 246* (NY). **Pichincha:** Cantón Quito, Parroquia Calacali, Reserva Geobotánica Pululahua, alrededores de Pailon, 25 sep. 1987, *Cerón 2253* (CTES, MO); ad margen viae ad flumen Machángara pr. Quito, 16 abr. 1920, *Holmgren 522* (G); côté de Guápulo, 20 mar. 1930, *Benoist 2195* (P); in *Andibus Ecuadorensibus*, 1861, *R. Spruce 5997* (G); vicinity of Guápulo, 31 mayo 1939, *Asplund 6639* (G, P); Quito, sin fecha, *Jameson 792* (G). PERU. Sin localidad, sin fecha, *Mattheros 1502* (BR). **Amazonas:** Leimabamba, 13 dic. 1962, *Woytkowski 7757* (MO). **Cajamarca:** camino a la Laguna Chamis, 11 jun. 1971, *Sánchez Vega 759* (CTES, SI). **La Libertad:** Sartinbamba, Marcabal, 26 feb. 1949, *Infantes Vega 1902* (LIL), 18 ago. 1952, *Infantes Vega 3738* (LIL).

En esta especie no se manifiesta un claro dimorfismo floral, pero se incluye en el subg. *Ebelia* por sus inflorescencias de ramificación cimosa y sus frutos de mericarpos indehiscentes.

6. *Galianthe hispidula* (A. Rich. ex DC.) E. L. Cabral & Bacigalupo, comb. nov. Basónimo: *Diodia hispidula* A. Rich. ex DC., Prodr. 4: 565. 1830. TIPO: Brasil. Brésil Leandro do Sacramento 103, año 1819 (holótipo, P no visto, foto F37153 CTES, SI). Figura 7.

Diodia paradoxa Cham., Linnaea 9: 216. 1834. TIPO: Brasil. Brasilia, Sellow (holótipo, B destruido, foto F869, CTES, SI); Brasil. Minas Gerais: 23-I-1846, *Widgren 1025* (neótipo, aquí designado, BR).

Sufrútice rizomatoso, de tallos simples, de 30–60 cm de alt., tetrágonos, alados, glabros o raramente pilosos sobre los ángulos o con escasas emergencias o lacinias con pelo apical. Hojas 35–100 × 15–35 mm, discoloras, vinosas al envejecer, elípticas u ovals, de ápice agudo o acuminado y base obtusa, atenuada en pseudopécíolo, con 5–8 pares de nervios secundarios, ligeramente curvos y paralelos, haz glabra o escabriúscula sobre toda la lamina o sólo sobre los nervios y bordes; vaina estipular escabriúscula o pilosa, con 5–9 lacinias hasta 10–13 mm long., glabras o algo escabriúsculas en la base. Inflorescencia cimoidal, monocasial a pleiocasial, con paracladios en gran parte cincinoides, con inflorescencias parciales contraídas, fasciculadas. Flores hipanto turbinado, escabriúsculo. Cáliz 4-partido, de 2 sépalos de 2.5–3 mm long, triangular-subulados, alternando con otros 2 sépalos menores y algún dientecito intercalar, glabro, de borde escabriúsculo, o rara vez también con alguna papila en el dorso de los sépalos. Corola blanca, 4-lobada, 3.8–4.6 mm long., de lóbulos más cortos que el tubo. Flor brevistila: superficie interna de la corola con pelos dispersos sobre el tubo y base de los lóbulos, anteras 0.8–1.2 mm long., estilo 0.8–1.6 mm long. y ramas estilares de 1 mm. Flor longistila: superficie interna

de la corola, con pelos moniliformes gruesos sobre los lóbulos y delgados sobre el tubo; anteras 0.8 mm long., estilo 3.5–4.5 mm long., ramas estilares de 1–1.2 mm. Fruto subhemisférico, 1.6–2 mm long., de superficie escabriúscula a glabra. Semilla de color castaño oscuro, 1.4–1.6 mm long., con estrofiolo rodeado por surco profundo.

Distribución (Fig. 11). Hierba umbrófila, habita en bosques y selvas del sur del Brasil, Paraguay y NE de la Argentina. Florece y fructifica desde la primavera hasta entrado el otoño.

Material seleccionado. BRASIL. **Minas Gerais:** Caldas, *Regnell 1 178* (P), 1845, *Widgren 202* (K); Bandeira do Sul, 20 ene. 1980, *Krapovickas et al. 35405* (CTES). **Paraná:** Porto Helena, 1 feb. 1949, *Schwarz 7425* (CTES); Campo Nov. Laranjeiras do Sul, 8 dic. 1968, *Hatschbach 20563* (NY). **Rio de Janeiro:** Nova Friburgo, morro da Caledonia, 8 jun. 1977, *Martinelli 2538* (RB). **Rio Grande do Sul:** Reserva Nonoai, 7 dic. 1974, *Porto 1186* (CTES, ICN). **Santa Catarina:** Itapiranga, San Antonio, 12 nov. 1964, *L. Smith et al. 13193* (LP), 6 feb. 1951, *Rambo 49879* (US). PARAGUAY. **Alto Paraná:** Irala, 1 dic. 1950, *Montes 11101* (CTES, LP). ARGENTINA. **Misiones:** in distr. urb. Posadas, praecipue in vicin. coloniae Bonpland, sin fecha, *W. Lillieskold s.n.* (G); L. N. Alem, Alem, Camping Municipal, 22 nov. 1986, *Cabral et al. 496* (CTES); Gral. Belgrano, San Antonio, nov. 1949, *Grondona et al. 3273* (BAB); Cainguaás, Ayo. Cuna, Pirú, 8 km de A. del Valle hacia Jardín de América, 8 dic. 1983, *J. Hunziker et al. 10896* (SI); Ayo. Solito, nov. 1949, *Martínez Crovetto & Leguizamón 5834* (BAB, SI); Candelaria, Bonpland, Ayo. Mártires, 18 dic. 1983, *Cabral et al. 431* (CTES), 18 mayo 1909, *Jørgensen 27* (BAB); Guaraní, El Paraiso y Ruta 2, 23 set. 1993, *Rodríguez et al. 754* (CTES); Orilla R. Bonito, 8 km desembocadura R. Uruguay, 7 dic. 1983, *Hunziker et al. 10824* (CTES); 14 km de El Soberbio, 6 dic. 1983, *Hunziker et al. 10801* (SI); Iguazú, Reserva Apepú, 4 mar. 1982, *Ferraro 2463* (CTES); Ayo. Uruguai, nov. 1949, *M. Crovetto et al. 5777* (BAB, SI); Parque Nacional Iguazú, 11 ene. 1972, *Mroginski et al. 300* (CTES), 1 dic. 1993, *Vanni et al. 3082* (CTES), 15 nov. 1976, *Guaglianone 174* (SI); 8 km del cruce de Libertad, Salto Uruguai, 9 dic. 1983, *Hunziker et al. 10903* (SI); Ayo. Uruguai, 35 km de Pto. Bemberg, 5 feb. 1951, *Capurro 868* (BA); Río Uruguai, Yacú Poí, 25 oct. 1949, *Perrone* (BA 54548), 28 nov. 1884, *Niederlein 366* (BA); Ayo. Uruguai, km 10, 14 ene. 1963, *Partridge s.n.* (BA 61693); Oberá, 24 dic. 1970, *Mroginski 80* (CTES); San Ignacio, km 101, 20 dic. 1945, *Schwarz 1699* (CTES); San Ignacio, 11 dic. 1941, *Biraben 5324* (LP); Salto Tabay, 14 oct. 1977, *Cabrera et al. 28771* (SI); San Javier, S. Javier, nov. 1962, *Martínez Crovetto 9764* (SI), 8 dic. 1945, *Bertoni 2494* (CTES), 26 ene. 1976, *Krapovickas et al. 28905* (CTES, SI); Acaraguá, 19 nov. 1946, *Bertoni 3073* (CTES). **San Pedro:** Monte Carlo, 2 mayo 1951, *Montes 15207* (CTES); Parque Prov. Moconá, 23 abr. 1993, *Rodríguez et al. 557* (CTES). **Corrientes:** Santo Tomé, Ea. Timbó, 8 dic. 1981, *Tressens et al. 1598* (CTES).

A *Galianthe hispidula* se la reconoce fácilmente por ser esta una hierba sufruticosa, estolonífera, de tallos simples. Común en sotobosque.

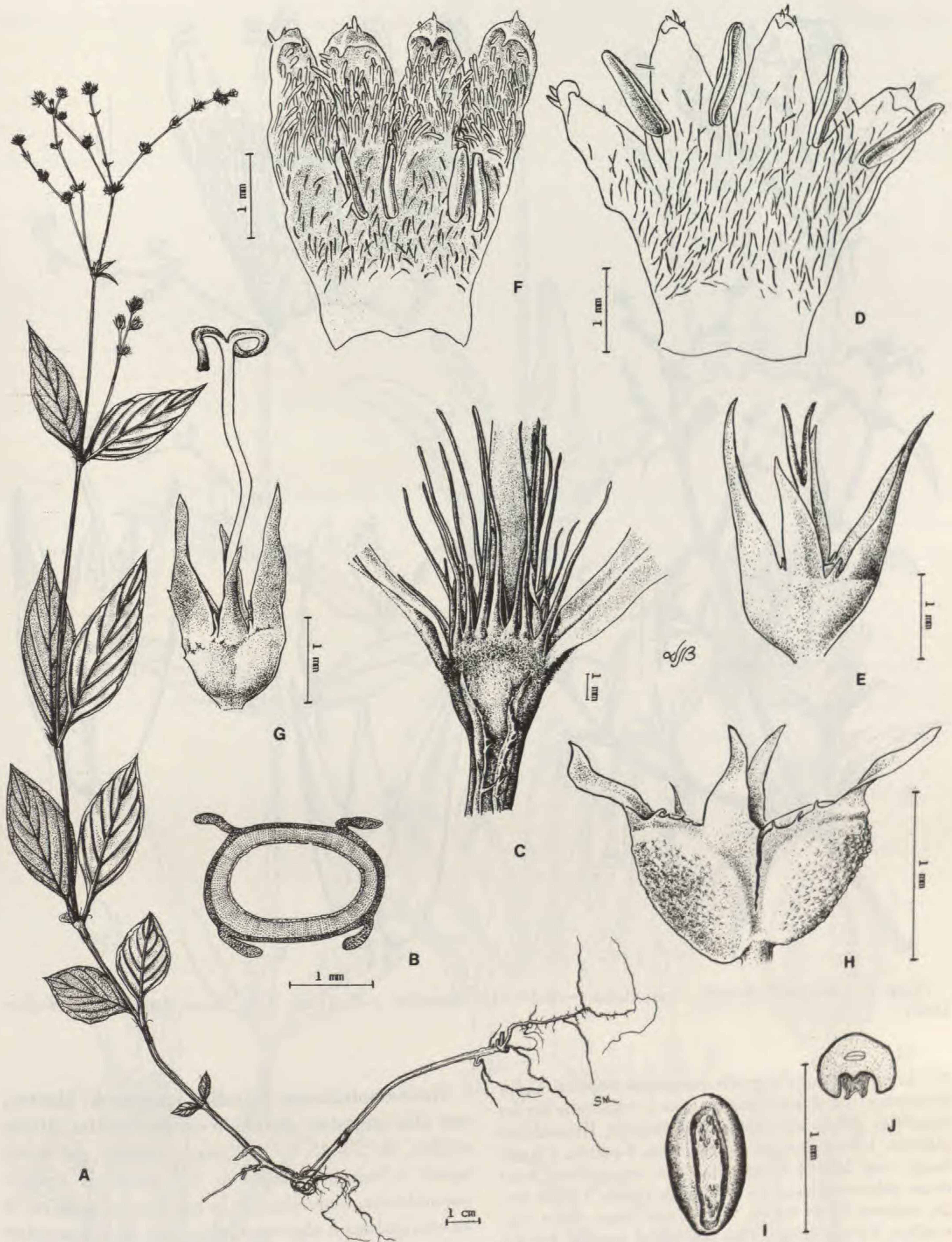


Figura 7. *Galianthe hispidula*. —A. Planta. —B. Corte transversal del tallo. —C. Vaina estipular. —D, E. Flor brevistila. —F, G. Flor longistila. —H. Fruto. —I. Semilla, cara ventral. —J. Corte transversal de semilla. A-C, F-J, Martínez Crovetto et al. 5777; D, E, Martínez Crovetto et al. 5834.

7. ***Galianthe humilis*** E. L. Cabral & Bacigalupo, sp. nov. TIPO: Brasil. Minas Gerais: Pouso Alegre, 2 mayo 1927, F. C. Hoehne 19357 (holótipo, SP). Figura 8.

Suffrutex caulibus tetragonis, glabris, anguste alatis, alis glabris vel scabriusculis. Folia sessilia 25-45 mm longa, 7-9 mm lata, elliptica, apice acuto, base attenuata, nervis secundariis 3-4 partibus, conspicuis, supra glabra vel scabriuscula. Vagina folii 3 mm longa aliqui pilosa,

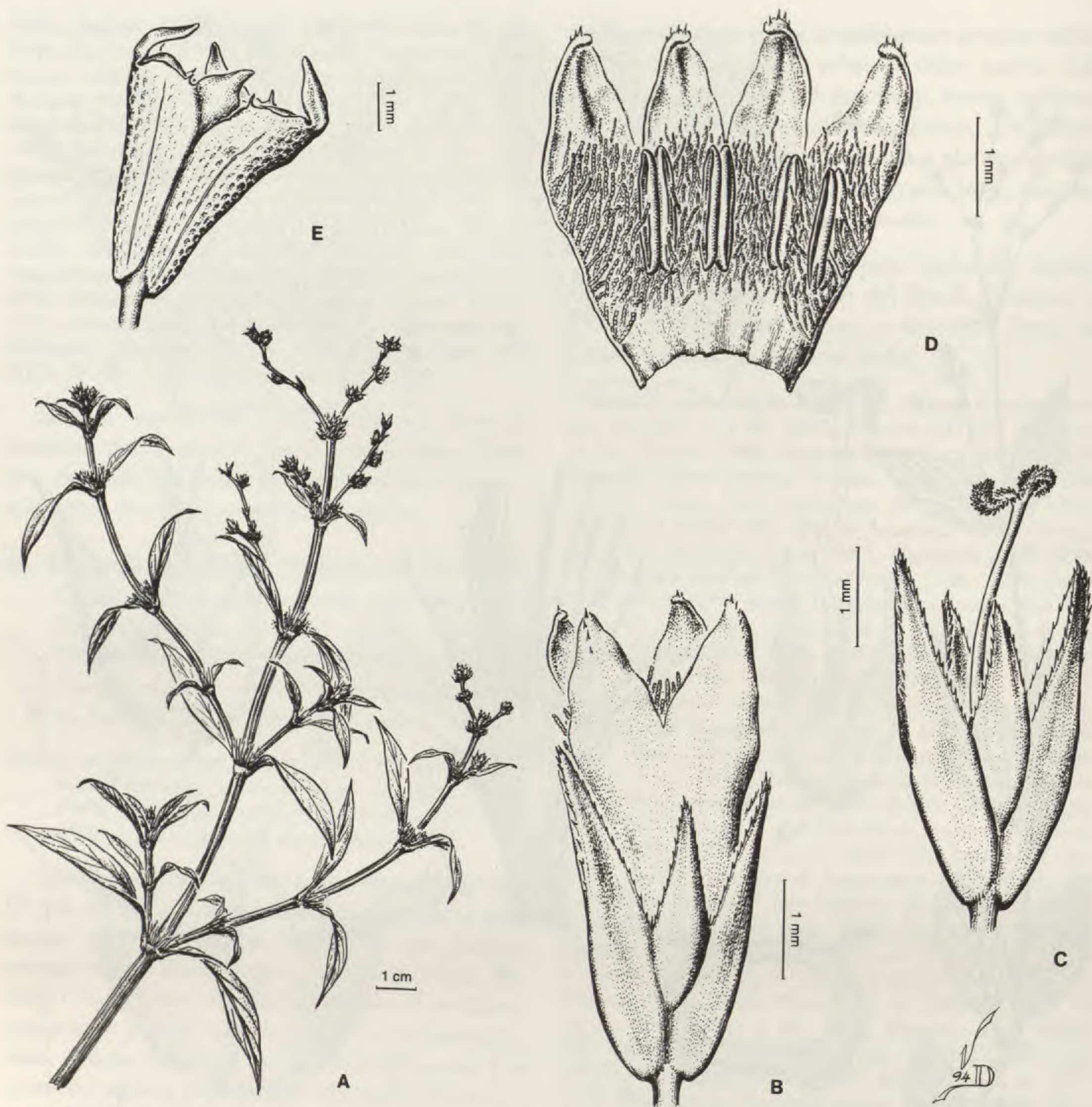
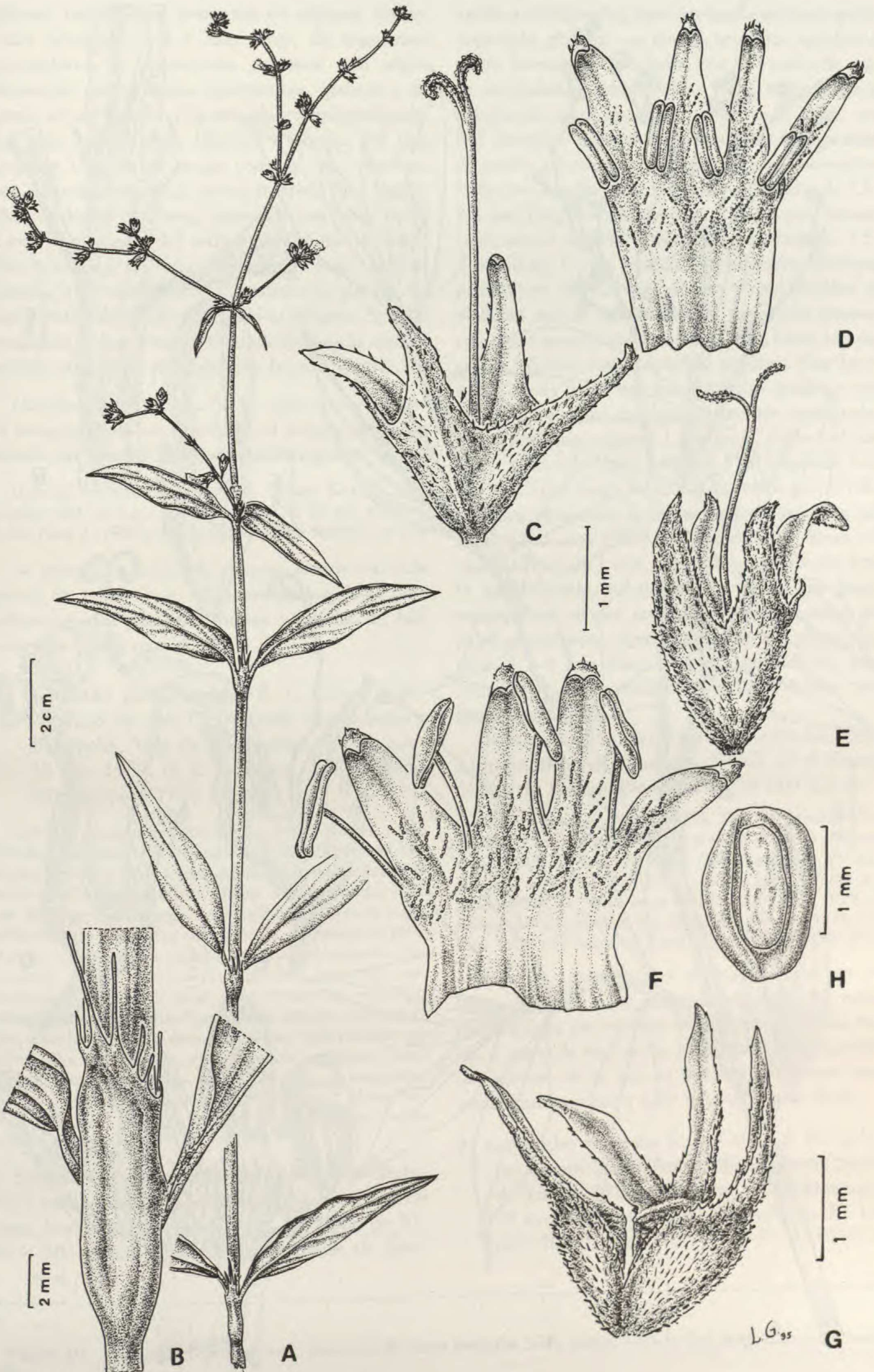


Figura 8. *Galianthe humilis*. —A. Rama. —B–D. Flor longistila. —E. Fruto. A–D, Souza León 11; E, Hoehne 19357.

3–7 laciniata. Flores in cymis compositis dispositi. Calyx tetrasetus, 1.2–2 mm longus, cum 2 segmentis leviter majoribus, glabris vel margine scabriusculo. Hypanthium glabrum, 1.8 mm longum. Corolla alba, 4-partita, 3.6 mm longa, cum lobulis tubus corollinus aequantibus, intus dense pubescentibus. Flos longistylus corolla 3.6 mm longa, antheris 1 mm longis, stylo 2 mm longo, ramis stigmatibus 0.6 mm longis. Flos brevistilus ignotus. Fructus 5 mm longus, subturbinatus, lateraliter aliquantum compressus, glaber, reticulato-foveolatus in sicco. Semen in maturum 3 mm longum, reticulato-foveolatum, strophiole faciem ventralem in parte tegente.

Hierba sufruticosa de tallos tetragonos, glabros, con alas angostas, glabras o escabriúsculas. Hojas sésiles, de 25–45 × 7–9 mm, elípticas, de ápice agudo y base atenuada con 3–4 pares de nervios secundarios, marcados en la haz y en resalto en el envés, glabras o algo escabriúsculas en la haz sobre todo hacia el margen, éste recurvado. Vaina estipular 3 mm de long., algo pilosa con 3–7 lacinias glabras, hasta de 4 mm long. Inflorescencia cimoidal con inflorescencias parciales fasciculadas, par-

Figura 9. *Galianthe polygonoides*. —A. Rama. —B. Vaina estipular. —C, D. Flor brevistila. —E, F. Flor longistila. —G. Fruto. —H. Semilla no madura, cara ventral. A–D, G, H, Braga 1741; E, F, Sucre 4190.





vifloras hasta flores solitarias en algunos nudos. Cáliz 4-partido, 1.2–2 mm long., de segmentos triangulares, 2 ligeramente mayores, con algún dientecito en los senos intercalares, glabros o de borde escabriúsculo. Hipanto glabro, subturbinado, 1.8 mm long. Corola blanca, 4-lobada, 3.6 mm long. de lóbulos tan largos como el tubo corolino, con densa pubescencia en su interior. Flor longistila: corola 3.6 mm long., anteras 1 mm long., estilo 2 mm long., ramas del estigma de 0.6 mm de largo. Flor brevistila: no vista. Fruto 5 mm long., subturbinado, algo comprimido lateralmente, glabro, oscuramente reticulado-foveolado al secarse. Semilla inmadura, 3 mm long., reticulado-foveolada con estrofiolo cubriendo parcialmente la cara ventral.

Distribución (Fig. 11). Se ha coleccionado hasta el momento sólo en Brasil, en el Estado de Minas Gerais, en campos altos, de suelos rocosos.

Material examinado. BRASIL. Minas Gerais: Carangola, 1400 m s.m., 20°43'S, 42°29'W, 22 jul. 1988, L. Souza Leon 11 (SPF); sin localidad, 1858, Weddell s.n. (G).

Se asemeja a *Galianthe cymosa*, siendo ésta más grácil, de tallos finos, minutamente papilosos, con inflorescencias parciales densas y corolas de lóbulos más cortos que el tubo.

8. *Galianthe polygonoides* E. L. Cabral & Bacigalupo, sp. nov. TIPO: Brasil. Rio de Janeiro: Petrópolis, Vale do Bonsucesso, 750 m s.m., 15 nov. 1969, D. L. S. Braga 1741 (holótipo, RB; isótipo, CTES). Figura 9.

Suffrutex scandens, caulibus fistulosis, glabris, ramis brevibus paucibus vel absentibus. Folia elliptica ad lanceolata 40–60 × 10–14 mm, glabra, margine revoluta scabriusculo. Vagina stipularis glabra conspicuissima 7–13 mm de largo, 6–7 laciniis, inaequalibus 1–5 mm de largo. Inflorescentia thyrsoides (monochasia, dichasia, vel pleochasia); inflorescentiis partialibus cymosis contractis, fasciculatis, interse distinctis (cincinndeis) hypanthio scabriusculo 1.5–2 mm de largo, calyx tetrasetus, segmentis triangularibus-subulatis. Corolla alba externe micropapillata, lobi dorso apicale dense papilloso, intus medium annulari pilis moniliformis, disco bipartito papilloso. Flores dimorfi. Fructus scabriusculus 2–2.5 mm, 2 mericarpis indehiscentibus, sepala persistente. Semina ± plana-convexa, strophiole faciem ventralem in parte in linea media tegente.

Sufrútice trepador, tallos fistulosos, subcilíndricos a tetrágonos, glabros, entrenudos de 6–9 cm de largo, brotes axilares escasos a nulos. Hojas de 40–60 × 10–14 mm, elípticas a lanceoladas, de ápice

agudo a acuminado y base atenuada en breve pseudopécíolo, glabras, con bordes revolutos, escabriúsculos, levemente discoloras, con 3–4 pares de venas secundarias subopuestas. Vaina estipular muy conspicua, tubulosa, glabra, 7–13 mm long., con 6–7 lacinias. Inflorescencia cimoidal (monocasial, dicasial o pleocasial), con paracladios cincinoides. Cáliz con 4 segmentos triangular-subulados de 1.5–2.5 mm long., escabriúsculos, a veces con dientes intercalares; hipanto obcónico, escabriúsculo, 1.5–2 mm long. Corola blanca, externamente micropapilada, con papilas más densas y más grandes en el dorso apical de los lóbulos; superficie interna, con pelos moniliformes sobre el tubo hasta la base de los lóbulos; disco bipartido papilloso. Flor brevistila: corola 3–3.2 mm long., lóbulos iguales o más cortos que el tubo corolino; filamentos estaminales 1–1.5 mm long., anteras 1 mm long., estilo 2–3 mm long., bifurcado en su extremo. Flor longistila: corola 3–3.5 mm long., lóbulos más cortos que el tubo corolino, filamentos estaminales muy breves y anteras 0.7–1 mm, estilo 3.5–4 mm long., ramas estilares filiformes 1 mm, densamente papilosas. Fruto subturbinado, escabriúsculo, 2–2.5 mm long., separándose en dos mericarpos indehiscentes, sépalos persistentes. Semilla más o menos plano-convexa, 1.7–2 mm long., cara ventral cubierta parcialmente por el estrofiolo en la línea media, cara dorsal foveolada.

Distribución (Fig. 11). Esta especie fue encontrada hasta el presente, sólo en Brasil, en el Estado de Rio de Janeiro, Petrópolis a 750–800 m s.m.

Material examinado. BRASIL. Rio de Janeiro: Petrópolis, 24 nov. 1968, D. Sucre et al. 4190 (RB); Caetetu, 1 jul. 1943, G. Goés et al. 240 (RB); Carangola, 29 ago. 1943, G. Goés et al. 500 (RB); Grota do Jacó, 800 m s.m., 2 nov. 1968, D. Sucre et al. 4013 (US), 2 dic. 1971, J. Barcia 349 (R); Araras, Ma. Comprida, 30 ene. 1971, Urbano 9927 (K); Serra da Estrella, 1844, Weddell 44 (P).

Galianthe polygonoides se individualiza por su hábito trepador y por la vaina estipular muy notable, tubulosa por encima de la inserción de las hojas, a modo de una ocrea, similar a la que presenta *G. vaginata* de la que se distingue por tener esta vainas pubescentes y tallo marcadamente alado.

9. *Galianthe vaginata* E. L. Cabral & Bacigalupo, sp. nov. TIPO: Brasil. Minas Gerais: Sierra do Itatiaia, ad marginem viae, ca. 1800 m s.m., 25 mayo 1902, P. Dusén 109 (holótipo, R). Figura 10.



Figura 11. Mapa de distribución de las especies de *Galianthe* subg. *Ebelia*.

Suffrutex erectus, caulibus tetragonis conspicue alatis. Folia 30–90 mm longa, 10–24 mm lata, discoloria, elliptica, apice acuto vel acuminato, base attenuata, nervis secundariis 4–5 paribus, supra glabra vel minute papillosa, subtus scabriuscula plerumque in nervis et marginibus. Vagina stipularis tubulosa, supra paribus foliorum suum prolongata, 6–12 mm longa, pubescentia, margine laciniata. Inflorescentiae cymoides, 1(2–3) verticillatae cum inflorescentiis partialibus fasciculatis, laxis. Flores dimorphi, hypantho turbinato, scabriusculo. Flos longistylus calice cum 4 segmentis deltoideo-subulatis: duobus 1.5–2 mm longis alterni cum duobus aliquod minoribus. Corolla alba, 4.5–4.7 mm longa, lobulis quam tubo brevioribus; tubo corollino usque lobulorum dimidiam partem disperse piloso. Antherae 1–1.2 mm longae cum filamentis brevissimis. Stylus 3.5–4.5 mm longus, ramis 0.8–1 mm longis. Flos brevistylus et fructus haud visus.

Sufrútice de tallos tetragonos notoriamente alados. Hojas de 30–90 × 10–24 mm, discoloras, elípticas, de ápice agudo o acuminado y base atenuada, con 4–5 pares de nervios secundarios, haz glabra con diminutas papilas sobre los nervios, enés escabriúsculo esencialmente sobre los nervios

y los bordes; vaina estipular tubulosa, prolongada por encima del par de hojas correspondiente, 6–12 mm de largo, pubescente, de bordes laciniados. Inflorescencia cimoidal con inflorescencias parciales fasciculadas, distanciadas entre sí. Flores heterostilas, hipanto turbinado, escabriúsculo. Flor longistila: cáliz de 4 segmentos triangular-subulados, 2 de 1.5–2 mm long. alternados con 2 ligeramente menores. Corola blanca, 4.5–4.7 mm long., de lóbulos más cortos que el tubo, con pelos dispersos en el interior del tubo corolino hasta la mitad de los lóbulos. Anteras 1–1.2 mm long., filamentos muy breves. Estilo 3.5–4.5 mm long., ramas estilares de 0.8–1 mm long. Flor brevistila y frutos no vistos.

Distribución (Fig. 11). Esta especie es brasileña y habita en los Estados de Minas Gerais y São Paulo.

Material examinado. BRASIL. São Paulo: Campos do Jordão, in campestribus dumetosis, ene. 1944, E. Frider-

ich S. J. s.n. (PACA 27764). Minas Gerais: prov. Minas Ad Caldas, 1867, A. Regnell I: 178 (BR).

ESPECIES DUDOSAS

Triodon polymorphus var. *intermedius* DC., Prodr. 4: 566. 1830. In Brasil meridionali, Sellow. TIPO: B, destruido. Probablemente existan duplicados no localizados. Su autor la caracteriza por sus hojas de tamaño intermedio.

Diodia polymorpha var. *floribunda* K. Schum., in Mart., Fl. Bras. 6(6): 13. 1888. TIPO: no designado, Brasil. Los ejemplares citados: "in provincia Rio de Janeiro prope Canta Gallo: Peckolt; Glaziou 3028; in silvis prope Gongo Soco: Bunbury; loco haud accuratius indicato: Sello 3433" B, destruidos. Duplicados no localizados. Según su autor se corresponde con plantas de hojas pequeñas, 5–13 × 1–4 mm, cáliz 2-mero.

Diodia polymorpha var. *lasiodisca* K. Schum., in Mart., Fl. Bras. 6(6): 12. 1888. TIPO: Brasil. "Habitā in provincia Minas Geraes prope Sumidorio: de Langsdorff" (holótipo, B destruido). No se han localizado duplicados.

Diodia polymorpha var. *densa* Zahlbr., Anz. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 12: 82. 1923. TIPO: Brasil. São Paulo (no visto). Duplicados no localizados.

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GÉNERO *GALIANTHE* SUBG.
EBELIA (RUBIACEAE:
SPERMACEAE): ESTUDIO
PALINOLÓGICO¹

*Stella Maris Pire*²

RESUMEN

Se estudia el polen de las especies de la tribu Spermaceae conocidas actualmente como: *Borreria anthospermoides* DC., *Diodia brasiliensis* Spreng., *D. cymosa* Cham., *D. hispidula* A. Rich. ex DC., *Knoxia dichotoma* Willd. ex Roem. & Schult. y *D. brasiliensis* var. *angulata* (Benth.) Standl., y se señala su afinidad con el polen del género *Galianthe* Griseb. Este estudio palinológico refuerza el criterio sustentado por Cabral y Bacigalupo de ampliar los límites del género *Galianthe* e incluir estas especies en el nuevo subgénero *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo, junto con *G. dichasia* (Sucre & C. G. Costa) E. L. Cabral, *G. humilis* E. L. Cabral & Bacigalupo y *G. polygonoides* E. L. Cabral & Bacigalupo, por sus frutos de mericarpos indehiscentes.

ABSTRACT

The pollen of the species of tribe Spermaceae currently known as *Borreria anthospermoides* DC., *Diodia brasiliensis* Spreng., *D. cymosa* Cham., *D. hispidula* A. Rich. ex DC., *D. dichotoma* (Willd. ex Roem. & Schult.) K. Schum., and *D. brasiliensis* var. *angulata* (Benth.) Standl. is studied, and its affinity with the pollen of the genus *Galianthe* Griseb. is indicated. This palynological study reinforces the suggestion of Cabral and Bacigalupo to extend the boundaries of the genus *Galianthe* to include the species listed above, because of their fruits with indehiscent mericarps, in the new *Galianthe* subg. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo, together with *G. dichasia* (Sucre & C. G. Costa) E. L. Cabral, *G. humilis* E. L. Cabral & Bacigalupo, and *G. polygonoides* E. L. Cabral & Bacigalupo.

Este trabajo es parte de un proyecto más amplio que comprende el estudio palinológico de toda la tribu Spermaceae. Esta es una de las tribus de Rubiaceae que incluye varios géneros conflictivos o críticos cuya delimitación es discutida, como *Spermaceae* L., *Diodia* L., *Borreria* G. F. W. Meyer, etc. (Steyermark, 1974; Verdcourt, 1976; Fosberg et al., 1981; Howard, 1989; Burger & Taylor, 1993, entre otros). El estudio palinológico pretende aportar datos que ayuden a la redefinición de los géneros, emprendimiento encarado junto con N. Bacigalupo y E. Cabral.

Hasta el momento se ha estudiado el polen de 145 especies representantes de la totalidad de los géneros (16) de las Spermaceae citadas para América. Al realizar este estudio se encontró que algunas especies del género *Diodia* L. poseen granos de polen con retículo complejo, éste es con un

suprarretículo y un infrarretículo a un nivel más bajo que el anterior. En Rubiaceae, este tipo de ornamentación, hasta el momento, sólo ha sido descrito para *Galianthe* Griseb. (Pire & Cabral, 1992). Este género ha sido recientemente revalidado por Cabral (1991).

Diodia, en sentido amplio, es un género que incluye taxones de caracteres muy dispares que no se corresponden con su definición genérica. Estos caracteres involucran al fruto, inflorescencia, morfología floral y también al polen. Bacigalupo y Cabral (inédito) reconocen, hasta el momento, 4 especies como válidas de *Diodia* (*D. virginiana* L., *D. kuntzei* K. Schum., *D. macrophylla* K. Schum. y *D. saponariifolia* Cham. & Schldl.), principalmente por presentar frutos indehiscentes, y proponen la reubicación de las restantes especies en otros géneros. El primer paso para la reubicación de las

¹ Esta comunicación constituye una parte del trabajo "Palynology of the Tribe Spermaceae (Rubiaceae)," presentado durante la International Conference on the Systematics of the Rubiaceae (1993), en St. Louis, Missouri. Expreso mi agradecimiento a las siguientes personas que me brindaron el material de estudio y aportaron valiosas sugerencias: E. Cabral, N. Bacigalupo (además, la lectura crítica del manuscrito) y R. Herbst. A las instituciones que otorgaron el apoyo financiero para este estudio: Universidad Nacional del Nordeste y CONICET. Mi reconocimiento, también para los directivos del IBONE por facilitarme el uso del Herbario y Biblioteca; lo hago extensivo a los curadores de los herbarios mencionadas en este trabajo.

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